Chapter 3

Closterium Nitzsch ex Ralfs

Northwest Washington taxa
Closterium abruptum West
Closterium acerosum Ehrenberg ex Ralfs
Closterium acerosum var. *elongatum* Brébisson
Closterium aciculare T. West
Closterium acutum Brébisson
Closterium acutum var. *variable* (Lemmermann) Willi Krieger
Closterium angustatum Kützing ex Ralfs
Closterium archerianum Cleve ex P. Lundell
Closterium baillyanum (Brébisson ex Ralfs) Brébisson
Closterium baillyanum var. *alpinum* (Viret) Gröblad
Closterium braunii Reinsch
Closterium closterioides (Ralfs) A. Louis & Peeters
Closterium closterioides var. *intermedium* (J. Roy & Bisset) Růžička
Closterium cf. *cornu* Ehrenberg ex Ralfs
Closterium costatum Corda ex Ralfs
Closterium cynthia De Notaris
Closterium dianae Ehrenberg ex Ralfs
Closterium dianae cf. var. *minus* Hieronymus
Closterium didymotocum Corda ex Ralfs
Closterium directum W. Archer
Closterium ehrenbergii Meneghini ex Ralfs
Closterium gracile Brébisson ex Ralfs
Closterium gracile f. *elongatum* (West & G. S. West) Kossinskaja

Closterium cf. *idiosporum* West & G. S. West
Closterium incurvum Brébisson
Closterium incurvum var. *latius* (Irénée-Marie) Irénée-Marie
Closterium cf. *jenneri* var. *robustum* G. S. West
Closterium juncidum Ralfs
Closterium kuetzingii Brébisson
Closterium leibleinii Kützing ex Ralfs
Closterium limneticum Lemmermann
Closterium limneticum var. *fallax* Růžička
Closterium lineatum Ehrenberg ex Ralfs
Closterium littorale F. Gay
Closterium lunula Ehrenberg & Hemprich ex Ralfs
Closterium moniliferum Ehrenberg ex Ralfs
Closterium navicula (Brébisson) Lütkemüller
Closterium nematodes Joshua
Closterium parvulum Nägeli
Closterium praelongum Brébisson
Closterium pritchardianum W. Archer
Closterium pronum Brébisson
Closterium pseudolunula Borge
Closterium pusillum Hantzsch
Closterium ralfsii var. *hybridum* Rabenhorst
Closterium cf. *rectimarginatum* A. M. Scott & Prescott
Closterium rostratum Ehrenberg ex Ralfs
Closterium setaceum Ehrenberg ex Ralfs
Closterium striolatum Ehrenberg ex Ralfs
Closterium venus Kützing ex Ralfs

Table 3.1: Key to *Closterium* Species.

I. Cell bow-shaped with fusiform (lens-shaped) center and long, beak-like apical extensions; apical pores present; cell wall finely striated (Figure 3.1)	Go to I (below)
II. Cell fusiform (lens-shaped) but without beak-like apical extensions; apical pores present or absent (Figure 3.1)	Go to II (page 58)
III. Cell crescent-shaped with tapered apex; curved along both lateral margins (may be asymmetric); apical pores present or absent; girdle bands mostly absent (Figure 3.1)	Go to III (page 60)
IV. Cell cylindrical with sides parallel at least in central portion of cell; apical pores present or absent (Figure 3.1)	Go to IV (page 64)
I. Cell bow-shaped with fusiform (lens-shaped) center and long, beak-like apical extensions; apical pores present; cell wall finely striated	
A Center of cell evenly inflated (symmetric); extensions long and delicate	
A.1 Cell center narrow (W<15 μm); chloroplast shorter than extensions	*Closterium setaceum* (Figures 3.174–3.177)
A.2 Cell center slightly wider (W>15 μm); chloroplast same length as extensions	*Closterium kuetzingii* (Figures 3.97–3.101)
B Center of cell asymmetric with curved dorsal margin; extensions relatively short and robust	*Closterium rostratum* (Figures 3.169–3.173)

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Table 3.1: Key to *Closterium* Species, continued

II. Cell fusiform (lens-shaped) but without beak-like apical extensions; apical pores present or absent	
A Cell straight with no perceptible curvature; cell wall smooth; apical pores absent	
A.1 Cell narrowly fusiform (L/W>10)	*Closterium* cf. *cornu* (Figures 3.48–3.50)
A.2 Cell broadly fusiform (L/W<10)	
A.2a Cell small (L<75 μm); chloroplast intact along lateral margin	*Closterium navicula* (Figures 3.128–3.131)
A.2b Cell larger (L>100 μm); chloroplast notched along lateral margin	*Closterium closterioides* (Figures 3.42–3.47)
B Cell very slightly curved (10–40°); cell wall smooth; apical pores present or absent[8]	
B.1 Apical pores present; cell narrowly fusiform or slightly crescent-shaped; chloroplast ends well below apex	*Closterium* cf. *idiosporum* (Figures 3.82–3.84)
B.2 Apical pores absent	
B.2a Cell large (L>200 μm); angular and broadly fusiform (L/W<10); chloroplast extends nearly to apex	*Closterium* cf. *rectimarginatum* (Figures 3.165–3.168)
B.2b Cell large (L>200 μm); narrowly fusiform, cylindrical at center (L/W>20); chloroplast ends well below apex	*Closterium pronum* (Figures 3.150–3.152)

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[8] Some taxa in this key are separated based on cell curvature (see Figure 3.6). This feature is quite variable so measure more than one cell and try alternate key options if you are having difficulty.

Table 3.1: Key to *Closterium* Species, continued

B.2c Cell smaller (L<200 μm); narrowly fusiform, tapered (L/W>20); chloroplast ends well below apex	*Closterium acutum* (Figures 3.19–3.21)
C Cell slightly to moderately curved (30–90°); cell wall smooth or finely striated; apical pores present or absent	
C.1 Apical pore present; cell large, narrowly fusiform or crescent-shaped (L>400 μm), dorsal margin evenly curved; ventral margin inflated at center; cell wall finely striated	*Closterium ralfsii* var. *hybridum* (Figures 3.160–3.164)
C.2 Apical pore absent	
C.2a Cell large, broadly fusiform or crescent-shaped (L>300 μm); dorsal margin evenly curved; ventral margin straight or slightly inflated; cell wall very finely striated (appears smooth)	*Closterium lunula* (Figures 3.119–3.123)
C2.b Cell small (L<50 μm); broadly cylindrical or fusiform (L/W <10); curvature often irregular	*Closterium pusillum* (Figures 3.156–3.159)

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Table 3.1: Key to *Closterium* Species, continued

III. Cell crescent-shaped with tapered apex; curved along both lateral margins (may be asymmetric); apical pores present or absent; girdle bands mostly absent	
A Apical pores absent	
A.1 Cell wall coarsely striated; striations visible under low magnification	
A.1a Cell nearly straight at center then slightly to moderately curved to apex (30–90°); girdle bands present; vacuole with many small crystals	*Closterium costatum* (Figures 3.51–3.55)
A.1b Cell moderately to strongly curved (>100°), with similar curvature on both margins; girdle bands absent; vacuole with single large crystal	*Closterium archerianum* (Figures 3.30–3.31)
A.2 Cell wall finely striated; striations visible on empty cell at high magnification; vacuole with single large crystal	
A.2a Cell moderately to strongly curved on both margins (>100°); apex with thickened subapical ring	*Closterium nematodes* (Figures 3.132–3.135)
A.2b Cell moderately to strongly curved on dorsal margin (>100°); ventral margin curved or straight near center; apex without thickened ring	*Closterium cynthia* (Figures 3.56–3.59)
A.3 Cell wall finely striated; striations visible on empty cell at high magnification; vacuole with many crystals	

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Table 3.1: Key to *Closterium* Species, continued

	A.3a Cell large and robust (usually L>300 μm, L/W<10); dorsal margin slightly curved (30–90°); ventral margin nearly straight; apex narrowly truncated, appearing reflexed; pyrenoids axial	*Closterium pseudolunula* (Figures 3.153–3.155) compare to *Closterium acerosum* (Figures 3.10–3.15)
	A.3b Cell large (usually L>300 μm); dorsal margin slightly curved (30–90°); ventral margin nearly straight or inflated; apex broadly truncated, not appearing reflexed; pyrenoids scattered	*Closterium lunula* (Figures 3.119–3.123)
	A.3c Cell slightly smaller (usually L<300 μm); broadly crescent-shaped (L/W<10); dorsal margin moderately or strongly curved (usually >100°); ventral margin inflated; pyrenoids axial	*Closterium moniliferum* (Figures 3.124–3.127)
A.4	Cell walls smooth	
	A.4a Cell large, robust; (L>400 μm; L/W<10); dorsal margin moderately to strongly curved (>100°); ventral margin inflated; chloroplast extends nearly to apex; vacuole with many tiny crystals	*Closterium ehrenbergii* (Figures 3.74–3.77)
	A.4b Cell very narrowly crescent-shaped or sigmoid (L>150 μm; L/W>25); strongly curved or sigmoid (>130°); chloroplast ends well short of apex; vacuole with several crystals	*Closterium acutum* var. *variable* (Figures 3.22–3.25)

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Table 3.1: Key to *Closterium* Species, continued

		A.4c Cell medium sized (L=100–300 μm); dorsal margin slightly to moderately curved (30–90°) ventral margin nearly straight or inflated; chloroplast ends well below apex; vacuole with single crystal	*Closterium littorale* (Figures 3.116–3.118)
		A.4d Cell medium sized (L=100–300 μm); dorsal margin moderately to strongly curved (>100°); ventral margin curved or straight near center; chloroplast extends nearly to apex; vacuole with single crystal	*Closterium cynthia* (Figures 3.56–3.59)
		A.4e Cell small, robust (L<75 μm; L/W<10); strongly curved on both margins (>130°); chloroplast extends nearly to apex; vacuole with single crystal	*Closterium* cf. *jenneri* var. *robustum* (Figures 3.91–3.92)
B	Apical pores present		
	B.1	Cell wall finely striated; cell large (L>400 μm), dorsal margin slightly to moderately curved (30–90°); ventral margin inflated at center; chloroplast extends nearly to apex	*Closterium ralfsii* var. *hybridum* (Figures 3.160–3.164)
	B.2	Cell wall smooth; cell moderately large (L=150–250 μm); slightly to moderately curved (30–90°) but with straight center; chloroplast ends well below apex	*Closterium dianae* (Figures 3.60–3.66
	B.3	Cell wall smooth; cell small to moderately large (L=50–250 μm); strongly curved (>120°); difficult group with overlapping morphological features	

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Table 3.1: Key to *Closterium* Species, continued

B.3a Cell small (L<100 μm); very strongly curved or hemispherical (>150°); chloroplast extended nearly to apex; vacuole with one large crystal	*Closterium incurvum* (Figures 3.85–3.90)
B.3b Cell slightly larger (L=100-130 μm); moderately to strongly curved, but not hemispherical (100–170°); chloroplast ends well below apex; vacuole with several scattered crystals	*Closterium venus* (Figures 3.182–3.184)
B.3c Cell relatively large (L=110–200 μm); strongly curved with inflated ventral margin (140–170°); chloroplast ends well below apex; apex bluntly rounded; vacuole poorly defined, with many scattered crystals	*Closterium leibleinii* (Figures 3.102–3.104)
B.3d Cell relatively large (L=150–225 μm); strongly and evenly curved (140–170°), without inflated ventral margin; chloroplast ends well below apex; apex somewhat acute, with thickened wall; vacuole poorly defined, with several scattered crystals	*Closterium parvulum* (Figures 3.136–3.143)

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Table 3.1: Key to *Closterium* Species, continued

IV. Cell cylindrical with sides parallel at least in central portion of cell; apical pores present or absent	
A Cell wall coarsely striated; striations visible under low magnification	
A.1 Girdle bands and apical pores present	
A.1a Cell narrowly cylindrical in center; gently tapered near apex; apex broadly truncated and inflated (capitate)	*Closterium angustatum* (Figures 3.26–3.29)
A.1b Cell crescent-shaped or cylindrical in center, then tapered to apex; apex narrowly truncated	*Closterium striolatum* (Figures 3.178–3.181)
A.2 Girdle bands and apical pores absent	
A.2a Cell broadly cylindrical or crescent-shaped; striations formed by double rows of punctae	*Closterium braunii* (Figures 3.38–3.41)
A.2b Cell broadly cylindrical or crescent-shaped; striations formed by single vertical rows of punctae	*Closterium pritchardianum* (Figures 3.148–3.149)
B Cell wall finely striated; striations visible on empty cell at high magnification	
B.1 Girdle bands and apical pores absent; cells large (L>300 μm); dorsal margin slightly curved (30–90°); ventral margin nearly straight; apex narrow, truncated, appearing reflexed;	*Closterium acerosum* (Figures 3.10–3.15)

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Table 3.1: Key to *Closterium* Species, continued

B.2 Girdle bands and apical pores present	
B.2a Cell narrowly cylindrical with straight, parallel sides for most of length (L/W $>$20); apex tapered and slightly curved; cell wall faintly striated	*Closterium juncidum* (Figures 3.93–3.96)
B.2b Cell broadly cylindrical or crescent-shaped (L/W$<$15); and only slightly tapered at apex; network of fine punctae visible between striations	*Closterium didymotocum* (Figures 3.67–3.70)
B.3 Girdle bands present; apical pores absent	
B.3a Cell long and narrowly cylindrical or crescent-shaped (L$>$250 μm; L/W$>$15); apex truncated and recurved	*Closterium praelongum* (Figures 3.144–3.147)
B.3b Cell long and narrowly cylindrical or crescent-shaped (L$>$250 μm; L/W$<$15); apex truncated but not recurved	*Closterium lineatum* (Figures 3.112–3.115)
B.4 Girdle bands absent; apical pores present	
B.4a Cell narrowly cylindrical in center, then tapered to apex; cell relatively small (L$<$200 μm)	*Closterium abruptum* (Figures 3.7–3.9)
B.4b Cell narrowly cylindrical to apex; apex slightly inflated; cell larger (L$>$200 μm)	*Closterium directum* (Figures 3.71–3.73)

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Table 3.1: Key to *Closterium* Species, continued

C Cell walls smooth	
C.1 Apical pores present; girdle bands absent; cells long and narrowly cylindrical; untapered and straight until near apex	
C.1a Chloroplast covers only about half of cell length; cells very long and narrow (L>400 μm; L/W>70)	*Closterium aciculare* (Figures 3.16–3.18)
C.1b Chloroplast extends nearly to apex; cell length and L/W ratio varies (L=100–400 μm; L/W=25–110)	*Closterium gracile* (Figures 3.78–3.81)
C.2 Apical pores present; girdle bands absent; cells broadly cylindrical or crescent-shaped (L/W<20)	*Closterium baillyanum* Figures 3.32–3.37
C.3 Cell lacking both apical pores and girdle bands	
C.3a Cell long and narrowly cylindrical (LW>20 μm; L>150 μm); chloroplast extends nearly to apex; vacuole with single crystal	*Closterium limneticum* (Figures 3.105–3.111)
C.3b Cell long and narrowly cylindrical (LW>20 μm; L>100 μm); chloroplast ends well below apex; vacuole with several crystals	*Closterium acutum* (Figures 3.19–3.21)
C.3c Cell short and broadly cylindrical to broadly fusiform (L<50 μm; L/W <10)	*Closterium pusillum* (Figures 3.156–3.159)

Table 3.2: *Closterium* Cell Measurements.

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium abruptum†	min	12.8 μm	195.2 μm	39°	11.0
	med	13.2 μm	212.8 μm	45°	16.6
	max	17.7 μm	241.6 μm	51°	17.9
Closterium acerosum	min	37.9 μm	344.4 μm	31°	8.0
	med	43.9 μm	487.0 μm	45°	11.4
	max	58.2 μm	759.8 μm	61°	17.8
Closterium acerosum	min	61.8 μm	1143.8 μm	31°	16.6
var. *elongatum*†	med	65.3 μm	1375.8 μm	36°	21.1
	max	68.8 μm	1429.0 μm	41°	23.1
Closterium aciculare	min	5.5 μm	444.6 μm	8°	74.0
	med	6.5 μm	566.3 μm	10°	82.1
	max	8.4 μm	621.4 μm	11°	94.5
Closterium acutum	min	3.0 μm	101.4 μm	6°	24.2
	med	4.6 μm	158.4 μm	13°	32.7
	max	7.7 μm	206.2 μm	22°	40.8
Closterium acutum var. *variable*	min	6.0 μm	154.6 μm	132°	25.8
	med	6.5 μm	291.2 μm	166°	43.4
	max	7.8 μm	368.8 μm	179°	53.5
Closterium acutum var. A	min	4.3 μm	96.6 μm	130°	17.1
	med	5.3 μm	111.4 μm	149°	23.2
	max	6.5 μm	126.6 μm	170°	25.5
Closterium angustatum	min	15.1 μm	251.5 μm	27°	14.5
	med	21.6 μm	456.1 μm	42°	21.1
	max	28.4 μm	682.0 μm	50°	31.7

†*summary statistics based on <5 cells*

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Table 3.2: *Closterium* Cell Measurements, continued

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium archerianum†	min	–	–	–	–
	med	22.5 μm	285.4 μm	143°	12.7
	max	–	–	–	–
Closterium baillyanum	min	43.7 μm	322.3 μm	29°	7.0
	med	46.9 μm	463.1 μm	46°	9.8
	max	52.3 μm	680.1 μm	64°	15.6
Closterium baillyanum var. *alpinum*†	min	29.5 μm	440.6 μm	44°	14.9
	med	30.2 μm	488.3 μm	46°	16.2
	max	31.4 μm	613.2 μm	49°	19.5
Closterium braunii	min	45.4 μm	720.8 μm	27°	14.0
	med	49.8 μm	920.2 μm	39°	17.4
	max	68.2 μm	1326.2 μm	51°	25.3
Closterium closterioides	min	29.9 μm	176.0μm	–	5.1
	med	38.9 μm	225.3 μm	0	5.7
	max	68.6 μm	390.0 μm	–	6.8
Closterium closterioides var. *intermedium*	min	15.9 μm	94.2 μm	–	4.0
	med	24.6 μm	118.2 μm	0	4.9
	max	30.0 μm	165.0 μm	–	6.2
Closterium cf. *cornu*	min	7.5 μm	90.9 μm	–	11.9
	med	7.8 μm	105.1 μm	0	13.0
	max	9.8 μm	151.2 μm	–	15.4
Closterium costatum	min	20.6 μm	205.0 μm	45°	7.1
	med	45.6 μm	364.9 μm	77°	8.1
	max	49.0 μm	504.4 μm	90°	12.9

†*summary statistics based on <5 cells*

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Table 3.2: *Closterium* Cell Measurements, continued

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium cynthia	min	9.8 μm	93.4 μm	138°	7.2
	med	12.8 μm	104.8 μm	142°	8.4
	max	13.8 μm	115.5 μm	162°	10.6
Closterium dianae	min	14.5 μm	160.8 μm	92°	10.1
	med	16.2 μm	199.5 μm	106°	11.1
	max	18.0 μm	247.2 μm	126°	14.7
Closterium cf. *dianae*†	min	13.3 μm	187.7 μm	65°	11.7
	med	16.6 μm	227.8 μm	72°	13.8
	max	22.3 μm	270.7 μm	102°	14.6
Closterium dianae cf. var. *minus*	min	10.9 μm	132.8 μm	90°	11.9
	med	11.4 μm	158.6 μm	116°	13.1
	max	16.4 μm	208.0 μm	147°	14.6
Closterium didymotocum	min	48.0 μm	422.7 μm	44°	7.9
	med	50.3 μm	516.3 μm	46°	10.1
	max	54.5 μm	591.2 μm	50°	11.8
Closterium directum	min	12.5 μm	225.2 μm	25°	12.1
	med	16.5 μm	292.6 μm	42°	18.9
	max	21.3 μm	407.4 μm	54°	26.5
Closterium ehrenbergii	min	75.9 μm	442.8 μm	86°	4.7
	med	95.7 μm	533.2 μm	111°	5.5
	max	148.8 μm	702.4 μm	145°	6.9
Closterium gracile	min	4.9 μm	168.8 μm	14°	27.4
	med	5.9 μm	212.4 μm	21°	32.5
	max	8.6 μm	272.0 μm	26°	40.8

†*summary statistics based on <5 cells*

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Table 3.2: *Closterium* Cell Measurements, continued

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium gracile f. *elongatum*	min	3.6 μm	199.8 μm	13°	44.4
	med	4.1 μm	340.8 μm	18°	86.0
	max	4.6 μm	426.4 μm	34°	107.1
Closterium cf. *idiosporum*	min	6.9 μm	190.7 μm	17°	19.1
	med	7.8 μm	221.2 μm	23.5°	26.6
	max	11.3 μm	244.6 μm	33°	33.0
Closterium incurvum	min	8.8 μm	66.1 μm	141°	7.1
	med	10.5 μm	87.4 μm	174°	8.3
	max	11.6 μm	100.4 μm	178°	9.0
Closterium incurvum var. *latius*	min	15.3 μm	84.2 μm	161°	5.5
	med	15.8 μm	93.3 μm	171°	5.9
	max	16.2 μm	96.3 μm	180°	6.0
Closterium cf. *jenneri* var. *robustum*†	min	11.3 μm	55.6 μm	138°	4.9
	med	11.3 μm	58.8 μm	138°	5.2
	max	11.3 μm	62.0 μm	139°	5.5
Closterium juncidum	min	6.0 μm	145.9 μm	33°	18.9
	med	8.0 μm	243.5 μm	36°	27.4
	max	15.0 μm	405.3 μm	40°	31.6
Closterium kuetzingii	min	16.0 μm	257.8 μm	16°	15.1
	med	20.1 μm	405.1 μm	29°	18.8
	max	31.6 μm	587.6 μm	47°	34.2
Closterium leibleinii	min	17.2 μm	118.9 μm	145°	5.8
	med	19.7 μm	147.7 μm	158°	7.7
	max	24.7 μm	189.8 μm	171°	8.6

†*summary statistics based on <5 cells*

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Table 3.2: *Closterium* Cell Measurements, continued

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium limneticum	min	4.4 μm	253.7 μm	6°	34.5
	med	6.9 μm	400.2 μm	11°	60.3
	max	8.4 μm	493.2 μm	23°	91.0
Closterium limneticum var. *fallax*	min	8.4 μm	155.8 μm	22°	18.4
	med	12.6 μm	284.4 μm	35°	20.9
	max	15.6 μm	299.6 μm	42°	24.0
Closterium lineatum	min	11.3 μm	320.1 μm	19°	28.3
	med	16.5 μm	600.2 μm	22°	36.3
	max	22.3 μm	897.6 μm	35°	40.3
Closterium littorale	min	15.5 μm	121.0 μm	49°	7.8
	med	16.2 μm	144.6 μm	68°	8.9
	max	18.6 μm	174.2 μm	79°	9.8
Closterium lunula	min	53.3 μm	325.5 μm	31°	4.4
	med	87.0 μm	628.5 μm	52°	7.1
	max	99.5 μm	1074.0 μm	66°	10.8
Closterium moniliferum	min	28.4 μm	185.2 μm	91°	5.3
	med	39.8 μm	263.8 μm	116°	6.5
	max	49.8 μm	328.0 μm	156°	8.0
Closterium navicula	min	11.7 μm	32.4 μm	–	2.7
	med	15.2 μm	50.7 μm	0	3.4
	max	17.5 μm	73.4 μm	–	4.5
Closterium nematodes	min	18.1 μm	259.3 μm	112°	9.4
	med	26.7 μm	287.5 μm	125°	11.1
	max	27.6 μm	304.0 μm	133°	15.1

†*summary statistics based on <5 cells*

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Table 3.2: *Closterium* Cell Measurements, continued

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium parvulum	min	15.8 μm	149.0 μm	106°	8.1
	med	17.3 μm	165.3 μm	135°	9.6
	max	21.1 μm	211.2 μm	151°	10.1
Closterium cf. *parvulum* var. A	min	33.6 μm	244.0 μm	139°	6.9
	med	37.1 μm	307.6 μm	146°	8.1
	max	38.9 μm	319.8 μm	158°	8.6
Closterium cf. *parvulum* var. B	min	17.7 μm	117.1 μm	155°	6.5
	med	18.7 μm	135.7 μm	166°	7.2
	max	20.4 μm	147.5 μm	174°	7.5
Closterium praelongum	min	13.2 μm	274.8 μm	24°	17.1
	med	20.8 μm	582.0 μm	31°	23.6
	max	36.6 μm	756.2 μm	35°	39.1
Closterium pritchardianum†	min	27.6 μm	520.0 μm	49°	13.0
	med	33.8 μm	529.6 μm	50°	16.3
	max	40.0 μm	539.2 μm	52°	19.5
Closterium pronum	min	5.9 μm	211.4 μm	12°	30.8
	med	8.0 μm	399.5 μm	12°	48.5
	max	10.7 μm	451.7 μm	16°	55.8
Closterium pseudolunula	min	43.2 μm	282.0 μm	45°	5.7
	med	49.2 μm	313.2 μm	54°	6.4
	max	55.1 μm	398.9 μm	83°	9.2
Closterium pusillum	min	8.2 μm	30.8 μm	57°	3.6
	med	8.9 μm	35.4 μm	83°	4.0
	max	9.9 μm	52.7 μm	94°	6.4

†*summary statistics based on <5 cells*

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Table 3.2: *Closterium* Cell Measurements, continued

		Cell Width	Cell Length	Curve	L/W Ratio
Closterium ralfsii var. *hybridum*	min	35.7 μm	415.0 μm	36°	11.2
	med	58.0 μm	731.8 μm	46°	12.6
	max	62.1 μm	914.4 μm	61°	16.0
Closterium cf. *rectimarginatum*	min	20.5 μm	149.2 μm	27°	7.3
	med	21.6 μm	187.9 μm	34°	8.9
	max	23.8 μm	225.6 μm	42°	10.3
Closterium rostratum	min	21.1 μm	189.8 μm	35°	7.5
	med	25.0 μm	298.9 μm	52°	12.1
	max	29.1 μm	500.2 μm	66°	18.3
Closterium setaceum	min	9.7 μm	259.4 μm	10°	24.2
	med	10.5 μm	323.0 μm	20°	31.2
	max	12.0 μm	424.8 μm	29°	36.6
Closterium striolatum	min	17.5 μm	221.0 μm	30°	8.8
	med	25.3 μm	316.9 μm	58°	11.9
	max	41.1 μm	532.2 μm	77°	16.9
Closterium venus	min	8.6 μm	103.6 μm	104°	8.6
	med	11.7 μm	112.8 μm	152°	9.8
	max	12.2 μm	128.4 μm	172°	12.5

†*summary statistics based on <5 cells*

Description

Closterium cells are mostly elongated and cylindrical, crescent-shaped, or fusiform, and circular in cross-section (Figure 3.1). The cells are usually curved and tapered toward the apex, which contains a terminal vacuole with one or more inorganic crystals of barium or strontium sulfate (Figures 3.2–3.5). The purpose of these crystals in not known. *Closterium* can be mistaken for a saccoderm desmid because the cells lack a median constriction (isthmus), but *Closterium* is a placoderm desmid because each cell is divided into mirror image semi-cells separated by a thin suture, and the semi-cells contain separate chloroplasts.

Closterium species identification can be challenging because many *Closterium* species are polymorphic or incompletely described in the taxonomic literature and different species may look very similar under low magnification. Before attempting to identify species of *Closterium*, it is essential that you examine more than one specimen, preferable from more than one site or collected on different dates. You may also need to collect length, width, and curvature data in order to make the correct identification.

Species identification is based primarily on cell shape, degree of curvature, chloroplast structure, number and placement of pyrenoids, number of inorganic crystals in the terminal vacuole, and cell wall properties. During cell division, some species develop one or more ring-like sutures at the point of semi-cell division. Cells may also develop girdle bands, which are wide, straight extensions of the mid-portion of the cell wall, or pseudo-girdle bands, which are extensions from the sutures, but look similar to true girdle bands (Figures 3.3–3.4). The cell wall may be smooth or striated with fine longitudinal ridges or coarse costae (Figure 3.5). Cell curvature, another important feature, can be estimated using two measurements as indicated in Figure 3.6. The curvature measurement usually represents the dorsal (outer) margin, which is often more strongly curved than the ventral (inner) margin. Straight or nearly straight cells may have only 10–20° of dorsal curvature while strongly curved cells may be nearly hemispherical (180°).

Closterium abruptum cells are long, cylindrical, and slightly curved (Figures 3.7–3.9). The cell margins are nearly straight in the mid-region, but become tapered near the apex. The apex is truncated or slightly rounded and lacks a pore. The terminal vacuoles are small, each containing a single large crystal. The cell wall is colorless to yellowish brown, usually has girdle bands and sutures, and appears to be smooth but should be very faintly striated. Each chloroplast contains an axial row of 4–6 pyrenoids and extends nearly to the apex of the semi-cell.

Closterium abruptum is usually found is slightly acidic, nutrient-poor sites. This species resembles *Closterium angustatum* (Figure 3.26) and *Closterium directum* (Figure 3.71), both of which are usually larger and less tapered near the apex.

Closterium acerosum cells are fusiform, nearly straight on the ventral margin, and slightly curved along the dorsal margin (Figures 3.10–3.15). The apex is abruptly narrowed, truncated or slightly rounded, and lacks an apical pore. It may appear reflexed due to the dissimilar curvatures of the dorsal and ventral margins. The terminal vacuoles are spherical and contain about 2–10 small crystals. The cell wall is colorless or yellowish brown, lacks true girdle bands (false girdle bands are occasionally present), and appears smooth but is usually very faintly striated. Each chloroplast contains an axial row of 5-30 pyrenoids and extends nearly to the apex of the semi-cell. ***Closterium acerosum* var. *elongatum*** is distinguished by its longer, more distinctly curved cells (Figures 3.13–3.15). According to Prescott et al. (1975), this variety may be invalid as it overlaps with morphological features found in the nominate variety.[9]

Closterium acerosum is widely distributed and can be found in eutrophic and polluted habitats as well as acidic or boggy ponds. *Closterium acerosum* resembles *Closterium braunii* (Figure 3.38) and *Closterium pritchardianum* (Figure 3.148, which can be distinguished by having rows of punctae rather than striations on the cell wall. Very careful examination is needed to distinguish *Closterium acerosum* from these other two species. Habitat is occasionally helpful because *Closterium acerosum* is more likely to be present in eutrophic and polluted habitats, but *Closterium acerosum* can also be collected in acidic or boggy ponds.

Closterium aciculare cells are cylindrical, exceptionally long, and narrow (Figures 3.16–3.18). The cells are nearly straight in the mid-region, then taper gradually to the gently curved apex. The apex is rounded, with a tiny apical pore and a long, indistinct vacuolated region containing a few small crystals. The cell wall is smooth, colorless, and lacks girdle bands. Each chloroplast is usually a simple, flat ribbon with approximately 5–20 axial pyrenoids, and occupies only about half the length of the semi-cell.

Closterium aciculare is typically planktonic and is common in eutrophic lakes and ponds. *Closterium aciculare* resembles *Closterium gracile* f. *elongatum* (Figure 3.80), which has sides that are parallel nearly to the apex; and *Closterium acutum* (Figure 3.19), which is usually much shorter than the other two taxa.

[9] *Closterium acerosum* var. *acerosum*

Closterium acutum cells are narrowly fusiform, tapering gradually from the center of the cell to the apex (Figures 3.19–3.25). The cells may be nearly straight or slightly curved, with the exception of *Closterium acutum* var. *variable* (see below), which has strongly curved crescent-shaped or sigmoid cells. The apex is narrowly truncated; lacks an apical pore; and contains a long, poorly defined terminal vacuole. The vacuoles contain one or more crystals; when multiple crystals are present, they may form bead-like chains. The cell wall is smooth and colorless and lacks girdle bands. Each chloroplast is a simple, flat ribbon, with 2–4 axial pyrenoids, and ends well below the apex. Most of the northwest Washington specimens were nearly linear with a length/width ratio $\geq$33 (Figures 3.19–3.21), which is an intermediate shape between the nominate variety[10] and a narrow variety, *Closterium acutum* var. *linea* (Perty) West & G. S. West. The major diagnostic feature used to separate the two forms is the length/width ratio, which is 20–33 for *Closterium acutum* var. *acutum* vs. 34–56 for *Closterium acutum* var. *linea* (Prescott, et al., 1975). Coesel and Meesters (2007) and Brook and Williamson (2010) question whether separating var. *linear* is valid, given that both forms are often present in the same sample.

Closterium acutum is common in eutrophic lakes and may form blooms. It resembles *Closterium aciculare* (Figure 3.16), *Closterium gracile* f. *elongatum* (Figure 3.80), and *Closterium pronum* (Figure 3.150), all of which are usually much longer than *Closterium acutum*.

Closterium acutum* var. *variable is characterized by strongly curved or twisted (sigmoid) cells, often with dissimilar curvature on opposite semi-cells (Figures 3.22–3.24). *Closterium acutum* var. *variable* was not especially common in the northwest Washington samples, but was found in similar eutrophic habitats as the nominate variety. ***Closterium acutum* var. A** specimens were collected from two artificial, alkaline, freshwater lakes located adjacent to an estuary (Figure 3.25). The cells may be morphological variations of *Closterium acutum* var. *variable*, but were shorter than other specimens of *Closterium acutum* var. *variable* and were collected in a very different habitat.

Closterium angustatum cells are long, cylindrical, and slightly curved (Figures 3.26–3.29). The cell sides are parallel through the mid-region, then gently tapered near the apex. The apex is truncated, thickened, slightly swollen (capitate) or recurved, and should have a distinct apical pore. The terminal vacuoles are spherical and contain one or more large, stacked crystal. The cell wall is yellowish brown and

[10] *Closterium acutum* var. *acutum*

has coarse striations (costae) with tiny pores visible between the striations; girdle bands are often present. Each chloroplast extends nearly to the apex and has 4–10 (or more) axial pyrenoids.

This species is usually found is slightly acidic, nutrient-poor sites. *Closterium angustatum* resembles *Closterium abruptum* (Figure 3.7), which is smaller and more evenly tapered; and *Closterium directum* (Figure 3.71), which is finely striated and lacks the expanded (capitate) apex.

Closterium archerianum cells are crescent-shaped, relatively narrow, strongly curved, and gradually tapered to the acutely rounded apex (Figures 3.30–3.31). The apex lacks an apical pore. The terminal vacuole is small and spherical, with a single large crystal or group of fused crystals. The walls are yellowish brown and distinctly striated. According to Prescott et al. (1975), the cell wall often has girdle bands, but this feature was not present in the northwest Washington specimen. Each chloroplast extends nearly to the apex and contains 5–8 axial pyrenoids.

Coesel and Meesters (2010) state that *Closterium archerianum* is associated with oligo-mesotrophic water, which is consistent with the site where the single specimen was collected (Storm Lake, Snohomish County, WA).

Closterium baillyanum cells are cylindrical and very slightly curved, usually with a nearly straight ventral margin and a more strongly curved dorsal margin (Figures 3.32–3.37). The apex is broadly truncate, slightly reflexed, with an apical pore. The terminal vacuoles contain many small crystals. The cell wall is colorless to dark brown, with a dark brown apex; lacks girdle bands; and appears smooth, but high magnification may show fine punctae. Each chloroplast extends nearly to the apex and contains 5–8 axial pyrenoids. ***Closterium baillyanum* var. *alpinum*** is distinguished by its narrower cells (Figures 3.36–3.37), but note that Brook and Williamson (2010) question whether the variety is valid, give the considerable morphological variation for the species.

Closterium baillyanum is found in slightly acidic meso-oligotrophic lakes and ponds. This species resembles *Closterium didymotocum* (Figure 3.67), which has distinctly striated walls with girdle bands.

Closterium braunii cells are long, cylindrical, and very slightly curved, with nearly parallel sides up to the abruptly tapered apex (Figures 3.38–3.41). The apex is abruptly narrowed, truncated, and lacks an apical pore. It may appear reflexed due to the dissimilar curvatures of the dorsal and ventral margins. The terminal vacuoles are spherical and contain many small crystals. The cell wall is brownish, lacks girdle bands, and appears coarsely striated; however, the striations are actually double rows of closely spaced punctae. Each chloroplast extends nearly to the apex and has 14–16 (or more) axial pyrenoids.

Closterium braunii is found in boggy, slightly acidic lakes and ponds. This species resembles *Closterium acerosum* (Figure 3.10), which lacks the distinctive double rows of punctae; and *Closterium pritchardianum* (Figure 3.148), which is striated with single (not double) rows of closely spaced punctae. Very careful examination is needed to distinguish *Closterium acerosum* from the other two species. Habitat is occasionally helpful because *Closterium acerosum* is more likely to be present in eutrophic and polluted habitats, but *Closterium acerosum* can also be collected in acidic or boggy ponds.

Closterium closterioides cells are straight and broadly fusiform, with rounded or truncated apices (Figures 3.42–3.47). The apex contains a well-defined spherical vacuole with numerous crystals. Although the apex wall is thickened, there does not appear to be an apical pore. The cell wall is smooth, colorless or brownish, and lacks girdle bands. Each chloroplast contains 3–6 axial pyrenoids and has distinctive lateral notches about half way between the apex and isthmus. ***Closterium closterioides* var. *intermedium*** was present in several mountain lake samples (Figures 3.45–3.47). This variety is quite difficult to distinguish from the nominate variety,[11] especially because it may be collected in the same sample (Figure 3.45). The primary distinguishing features for *Closterium closterioides* var. *intermedium* include slightly shorter cell lengths, lower L/W ratios, and fewer pyrenoids (2–3) compared to the nominate variety.

Closterium closterioides is usually found in slightly acidic water; all of the northwest Washington specimens were collected in oligo-mesotrophic or mesotrophic mountain lakes and ponds. The large size and notched chloroplasts make *Closterium closterioides* fairly distinctive, but small specimens of *Closterium closterioides* var. *intermedium* resemble *Closterium navicula* (Figure 3.128), which can be distinguished by its unnotched chloroplast.

Closterium cornu cells are narrowly fusiform, straight or slightly curved, with bluntly truncated apices that lack an apical pore (Figures 3.48–3.50). The terminal vacuoles are small and spherical, with single crystals. The cell wall is smooth, colorless, and lacks girdle bands. Each chloroplast extends nearly to the apex and contains 2–4 axial pyrenoids.

[11] *Closterium closterioides* var. *closterioides*

Closterium cornu is associated with slightly acidic, boggy lakes and ponds. This identification is uncertain because *Closterium cornu* is usually described as having a slightly curved dorsal margin, but all of the northwest Washington specimens have equally straight margins. This species resembles *Closterium acutum* (Figure 3.19), which is narrower; *Closterium pronum* (Figure 3.150), which is longer; and *Closterium idiosporum* (Figure 3.82), which has an apical pore.

Closterium costatum cells are large, robust, and broadly crescent-shaped (Figures 3.51–3.55). The mid-region along the ventral margin is often nearly straight or very slightly inflated while the dorsal margin is evenly curved. The apex is bluntly truncated and often slightly thickened (capitate), but with no apical pore. The terminal vacuoles are spherical and contain many tiny crystals (Figures 3.52–3.53) or a single large crystal (Figure 3.55). The cell wall is yellowish brown or reddish brown, with a darker brown apex, lacks girdle bands, and is coarsely striated with thick "costae." Each chloroplast extends nearly to the apex and contains many scattered pyrenoids.

Closterium costatum is usually associated with boggy, slightly acidic lakes and ponds. The coarse wall striations make this species is fairly distinctive, but it can be confused with *Closterium didymotocum* (Figure 3.67) and *Closterium striolatum* (Figure 3.178), both of which have girdle bands.

Closterium cynthia cells are crescent-shaped and moderately to strongly curved (Figures 3.56–3.59). The mid-section of the cell may be nearly straight or continuously curved; the sides may be nearly parallel until near the apex, or gently tapered across the length of the cell. The apex is broadly rounded and lacks a terminal pore. The terminal vacuole is spherical and contains a single large crystal. Each chloroplast extends nearly to the apex and contains 2–5 axial pyrenoids. The cell wall is highly variable, appearing colorless, yellowish, or brownish; smooth or very faintly striated; and with or without girdle bands and sutures. Smooth walled cells were separated by many taxonomists into a different species, *Closterium jenneri* Ralfs, which is otherwise morphologically identical to *Closterium cynthia*; both species are typically found in slightly acidic lakes and ponds. Růžička (1977) suggested that *Closterium jenneri* could be an immature form of *Closterium cynthia* (see discussion by Coesel and Meesters, 2007). In this guide, the striated specimens were merged with *Closterium cynthia* except for *Closterium jenneri* var. *robustum*, which is sufficiently different that it deserves separate treatment (see species discussion below). All of the northwest Washington specimens appeared to lack girdle bands and have smooth or very faintly striated walls. In addition to the possibly synoymy with *Closterium jenneri*, *Closterium cynthia* resembles *Closterium incurvum* (Figure 3.85), which is more strongly curved and usually smaller.

Closterium dianae cells are narrowly crescent-shaped and moderately or strongly curved (Figures 3.60–3.62). This species is highly polymorphic, but the northwest Washington specimens have straight, parallel sides through the mid-portion of the cell, becoming moderately curved and tapered approaching the apex. The apex is acutely rounded or obliquely tapered, with a thickened wall below the apex, and a small pore on the dorsal margin just below the apex. The terminal vacuole is relatively large and contains 2–10 (or more) small crystals dispersed throughout the vacuole. The cell wall is colorless or brownish, smooth, and lacks girdle bands. Each chloroplast ends slightly below the apex and contains 4–8 axial pyrenoids.

The specimens in Figures 3.63–3.64 may be ***Closterium dianae* cf. var. *minus***, which is characterized by small, strongly curved cells (cell length $\leq$150 μm; cell width $\leq$15 μm). The specimens in Figures 3.65–3.66 are also tentatively identified as *Closterium dianae*; this variety (or morphological form) is characterized by cells that are inflated at the center.

Closterium dianae can be found in slightly acidic, boggy ponds (Brook and Williamson, 2010), but the northwest Washington specimens were in small, mesotrophic lakes and ponds. *Closterium dianae* can resemble several other species of *Closterium*. The northwest Washington specimens are similar to *Closterium calosporum* Wittrock (no image available), which has a distinctive zygote that is needed for species identification; and *Closterium parvulum* (Figure 3.136), which is usually more strongly curved. Some of the specimens resemble *Closterium dianae* var. *pseudodianae* (J. Roy) Willi Krieger (see description by Růžička, 1977), but confirmation of this variety is not feasible.

Closterium didymotocum cells are cylindrical, nearly straight along the ventral margin, slightly curved along the dorsal margin, and only slightly tapered at the apex (Figures 3.67–3.70). The apex is broadly truncate, slightly thickened, and appears to have an apical pore. The terminal vacuole is spherical and contains many tiny crystals. The cell wall is yellowish-brown, becoming dark brown at the apex, and is faintly but distinctly striated, with a network of fine punctae between the striations. Both girdle bands and sutures were observed in most specimens. Each chloroplast extends nearly to the apex and contains many scattered pyrenoids.

Brook and Williamson (2010) state that the wall striations in *Closterium didymotocum* stop short of the apex, but Figure 3.69 shows that the striations in the northwest Washington specimens extend to the apex. In addition, Brook and Williamson suggest there may have been many incorrect identifications of *Closterium didymotocum* and the similar species, *Closterium baillyanum* (Figure 3.32). *Closterium baillyanum* is a common desmid in northwest Washington lakes, and can be distinguished by its lack of true girdle bands and smooth or very faintly striated walls. The northwest Washington specimens have very obvious girdle bands, so they were not assigned to *Closterium baillyanum*. All of the *Closterium didymotocum* specimens were collected from a single floating bog in British Columbia and may represent a new species or variety.

Closterium directum cells are narrowly cylindrical and straight or slightly curved (Figures 3.71–3.73). The sides are parallel along most of the cell, becoming only slightly tapered near the apex so that the apex is nearly as wide as the rest of the cell. The apex is broadly truncated, slightly reflexed, and lacks an apical pore. The terminal vacuole is small, spherical, and contains one large, compound crystal. The cell wall is colorless or yellowish, with true girdle bands, and is finely striated. Each chloroplast contains 6–20 axial pyrenoids and extends nearly to the apex.

Closterium directum is usually found in boggy, slightly acidic lakes and ponds. *Closterium directum* resembles *Closterium abruptum* (Figure 3.7), which is smaller and more evenly tapered; and *Closterium angustatum* (Figure 3.26), which has a coarsely striated wall and expanded (capitate) apex.

Closterium ehrenbergii cells are large and crescent-shaped, with a strongly curved dorsal margin and a moderately curved ventral margin that is inflated at the center of the cell (Figures 3.74–3.77). The sides are gradually tapered to the acutely rounded apex; the apex does not have an apical pore. The terminal vacuoles are large and spherical, containing many small crystals. The cell wall is colorless or brownish, lacks girdle bands, and usually appears smooth, but actually is finely striated; these striations are hard to see unless highly magnified. Each chloroplast extends nearly to the apex and contains many small, scattered pyrenoids.

Brook and Williamson (2010) suggest that *Closterium ehrenbergii* may be a "catch-all" species comprised of more than one undescribed species. Not surprisingly, it is found in a very wide range of habitats, and is especially common in nutrient enriched ponds and ditches, sometimes forming blooms. *Closterium ehrenbergii* is relatively easy to identify based in its large, crescent-shaped cells and numerous scattered pyrenoids, even if the form encompasses more than one species.

Closterium gracile cells are narrowly cylindrical, with parallel sides for most of the length of the cell (Figures 3.78–3.81). The cells are usually straight except near the apex, where they are gently curved and slightly tapered. The apex is truncated with a tiny pore. The terminal vacuoles are poorly defined and contain one or more crystals distributed throughout the vacuole. The cell wall is smooth, colorless or pale yellow, and lacks girdle bands but may have numerous sutures. Each chloroplast is a simple ribbon that extends nearly to the apex and has 4–7 (or more) axial pyrenoids.

Most of the *Closterium gracile* specimens were exceptionally long and narrow, fitting descriptions for ***Closterium gracile* f. *elongatum*** (Figures 3.80–3.81). Brook and Williamson (2010) argue against separating this as a variety because the nominate variety[12] has been shown to include specimens covering a gradient encompassing both long and short morphological forms. In addition, AlgaeBase lists *Closterium gracile* f. *elongatum* as a synonym for *Closterium gracile* (Guiry & Guiry, 2023). However, the long and short northwest Washington specimens were collected from different locations, so *Closterium gracile* f. *elongatum* was separated from *Closterium gracile* in Table 3.2.

Closterium gracile is generally found in slightly acidic lakes and ponds; the elongated form was particularly abundant in Summer Lake, a floating sphagnum bog in Skagit County, WA. Short *Closterium gracile* cells (Figure 3.78) resemble *Closterium limneticum* (Figure 3.105) and *Closterium acutum* (Figure 3.19), both of which are more uniformly tapered. *Closterium gracile* f. *elongatum* (Figure 3.80) resembles *Closterium aciculare* (Figure 3.16), which has long, uniformly tapered cells and chloroplasts that do not extend to the apex.

Closterium idiosporum cells are narrowly fusiform or very slightly crescent-shaped, nearly straight (sometimes asymmetrically curved), tapering gradually from the center of the cell to the apex (Figures 3.82–3.84). The apex is truncate, with a tiny apical pore. The terminal vacuoles are long and poorly defined, with several small crystals that may be irregularly distributed or form short chains. The cell wall is colorless, smooth, and lacks girdle bands. Each chloroplast stops well below the apex and contains 3–4 axial pyrenoids.

Closterium idiosporum is described as being found in slightly acidic lakes and ponds (Brook and Williamson, 2010), which is consistent with the sites where the northwest Washington specimens were collected. Without the presence of zygotes,

[12] *Closterium gracile* var. *gracile*

however, species confirmation is difficult. *Closterium idiosporum* resembles *Closterium acutum* (Figure 3.19), which is smaller, and *Closterium gracile* (Figure 3.78), which has parallel sides and a small terminal vacuole.

Closterium incurvum cells are relatively small, crescent-shaped (Figures 3.85–3.90). The cells are very strongly curved ($\geq$170°), with an evenly curved ventral margin that lacks any median inflation. The apex is acute, with a small pore just below the apex on the dorsal side. The terminal vacuole is well-defined and contains one or more large crystals. The cell wall is colorless, smooth, and lacks girdle bands. The chloroplast extends nearly to the apex and has 1–3 large, axial pyrenoids. ***Closterium incurvum* var. *latius*** was present at several locations (Figures 3.89–3.90). This variety has slightly wider cells, which gives it a more robust appearance.

Closterium incurvum has a wide habitat tolerance, and many of the northwest Washington specimens were collected in mesotrophic or eutrophic sites. *Closterium incurvum* cells are very similar to *Closterium parvulum* (Figure 3.136), and *Closterium venus* (Figure 3.182). Both species are characterized by strongly curved, crescent-shaped cells with nearly the same size ranges for length and width. Both species can be present at the same site (Figure 3.88; Sovran, et al., 2013), so habitat does not help with separation. Despite the morphological similarity of the vegetative cells, the separation between *Closterium venus* and *Closterium incurvum* is supported by differences in their zygotes (Cook, 1963). The best visual features for separating these two species is the dorsal curvature, which is nearly hemispherical for *Closterium incurvum* vs. crescent-shaped for *Closterium venus*; and the chloroplast length, which extends nearly to the apex in *Closterium incurvum* cells, but ends well below the apex in *Closterium venus* cells.

Closterium jenneri* var. *robustum cells are small, crescent-shaped, and moderately curved (Figures 3.91–3.92). The apex is broadly rounded and lacks an apical pore. The terminal vacuole is spherical and contains a single large crystal. The cell wall is colorless or brownish, usually appears to be smooth, and lacks girdle bands. Each chloroplast extends nearly to the apex and contains 2–3 axial pyrenoids.

Closterium jenneri is a confusing species and all of the nominate variety[13] specimens were merged with *Closterium cynthia* (see discussion above). The specimens in Figures 3.91–3.92 are sufficiently distinctive that they were not merged with *Closterium cynthia*, and are instead presented as one of the described

[13] *Closterium jenneri* var. *jenneri*

varieties of *Closterium jenneri* (Prescott, et al., 1975). Only two specimens were collected, both from a small, high elevation snow-melt pond in the Mt. Baker Recreational Area. Additional specimens are needed to confirm the identification.

Closterium juncidum cells are narrowly cylindrical, slightly curved, tapered near the apex, with parallel sides in the mid-region (Figures 3.93–3.96). The apex is truncated, often oblique, and contains an apical pore. The terminal vacuole is small and spherical, with one large, compound crystal or several smaller crystals. The cell wall is colorless, yellow, or brown, and has true girdle bands, but this feature may be absent in young cells. The wall is striated, but this feature is also variable, so the cells may appear smooth. Each chloroplast extends nearly to the apex and contains 4–9 (or more) axial pyrenoids.

Closterium juncidum is generally found in slightly acidic, oligotrophic lakes and ponds. *Closterium juncidum* cells resemble *Closterium gracile* (Figure 3.78), which can be distinguished by its smooth, unstriated cell wall and *Closterium lineatum* (Figure 3.112), which is much larger and is more likely to be collected in mesotrophic waters.

Closterium kuetzingii cells are bow-shaped and nearly straight, with an inflated center, and long, narrow, beak-like extensions (Figures 3.97–3.101). The extensions are straight almost to the apex, then gently curved, giving the cell a symmetric appearance with equal dorsal and ventral curvature. Each extension is approximately as long as the combined length of both chloroplasts. The apex is usually slightly expanded and contains a small apical pore. The vacuoles are located at the upper end of each chloroplast near the base of the narrow extensions (subapical), and contain several small crystals. The cell wall is colorless, yellowish or brownish, lacks girdle bands, and is faintly striated; the striations are very fine, so the cell wall usually appears smooth. The chloroplasts are confined to the central fusiform portion of the cell and each contains 4–7 axial pyrenoids.

Closterium kuetzingii has a wide habitat tolerance, and some of the northwest Washington specimens were collected in mesotrophic sites while others were found in slightly acidic boggy ponds and lakes. *Closterium kuetzingii* can be difficult to distinguish from *Closterium setaceum* (Figure 3.174), especially because both species may be present in the same sample. The best separation feature is the greater length of the extensions in *Closterium setaceum*, which gives that species a more delicate appearance (see Figure 3.101).

Closterium leibleinii cells are strongly curved, crescent-shaped, and slightly inflated at the center (Figures 3.102–3.104). The apex is bluntly pointed, with a very small subapical pore located on the dorsal margin. The terminal vacuole is fairly large and contains many small crystals. The cell wall is smooth, colorless or very pale brown, and lacks girdle bands. Each chloroplast ends well below of the apex and contains 2–6 axial pyrenoids.

Closterium leibleinii is usually found in mesotrophic or eutrophic sites; many of northwest Washington specimens were collected in small residential ponds. This species closely resembled *Closterium moniliferum* (Figure 3.124), which can also be found in eutrophic sites, but is larger and lacks the subapical pore.

Closterium limneticum cells are narrowly cylindrical, with straight, parallel sides in the mid-section, then tapered and gently curved in the upper portion of the cell (Figures 3.105–3.111). The apex is narrowly rounded and lacks an apical pore. The terminal vacuole is spherical or slightly elongated, usually containing only one crystal. The cell wall is colorless, smooth, and lacks girdle bands. The chloroplasts extend nearly to the apex and contains 3–5 (or more) axial pyrenoids. In addition to the nominate variety,[14] the northwest Washington samples contained ***Closterium limneticum*** var. ***fallax*** (Figures 3.109–3.111), which is a shorter and wider (fusiform) variation compared to the nominate. The northwest Washington specimens for both varieties had lengths and widths that were outside the ranges listed by Prescott et al. (1975); however, this species exhibits considerable morphological variability with respect to length.

Closterium limneticum closely resembles *Closterium gracile* (Figure 3.78), which has a tiny apical pore. One of the best features for separating these two species is habitat: *Closterium gracile* is usually collected in benthic samples and along shorelines in slightly acidic oligotrophic waters; *Closterium limneticum* is usually collected in plankton samples from eutrophic lakes (Brooke and Williamson, 2010).

Closterium lineatum cells are narrowly cylindrical, with straight, parallel sides throughout most of the cell length, then tapered and slightly curved near the apex (Figures 3.112–3.115). The apex is narrow and truncated, with a distinct apical pore. The terminal vacuole is small and spherical, with many crystals. The cell wall is finely striated, lacks girdle bands, and is colorless in young cells but usually yellowish or brownish in older cells. Each chloroplast extends nearly to the apex and contains 9–11 (or more) axial pyrenoids.

[14] *Closterium limneticum* var. *limneticum*

Closterium lineatum is generally found in mesotrophic lakes and ponds. *Closterium lineatum* is very similar in size and shape to *Closterium praelongum* (Figure 3.144), which can be distinguished by its recurved apex. *Closterium lineatum* also resembles *Closterium gracile* (Figure 3.78), which can be distinguished by its smooth, unstriated cell wall and *Closterium juncidum* (Figure 3.112), which is much smaller and is more likely to be collected in boggy, slightly acidic sites.

Closterium littorale cells are crescent-shaped and slightly curved, with a nearly straight or slightly inflated ventral margin and evenly curved dorsal margin (Figures 3.116–3.118). The apex is narrowly rounded, with a thickened wall and no apical pore. The terminal vacuole located below the thickened apex, at the top of the chloroplast. The vacuole usually contains a single large crystal. The cell wall is smooth, colorless, and lacks girdle bands. Each chloroplast extends nearly to the apex and contains 3–10 axial pyrenoids.

Closterium littorale has a wide habitat tolerance and can be found in boggy acidic sites, eutrophic lakes and ponds, and associated with submerged vegetation in streams and rivers (Brook and Williamson, 2010). All of the northwest Washington specimens were collected along the shoreline of creeks and rivers or in small ponds.

Closterium lunula cells are large and broadly fusiform or crescent-shaped, with a nearly straight or slightly inflated ventral margin and slightly curved dorsal margin (Figures 3.119–3.123). The apex is bluntly truncated and may appear recurved due to the uneven dorsal/ventral curvature. The terminal vacuole is spherical or oval (sometimes described as conical), lacks an apical pore, and contains many small crystals that may form stacked groups. The cell wall is colorless or brownish, lacks girdle bands, and may appear smooth, but is actually very finely striated. Each chloroplast extends nearly to the apex and contains many small, scattered pyrenoids.

Closterium lunula is usually found along the shoreline of slightly acidic, boggy lakes and ponds. The northwest Washington specimens were collected from a very broad range of habitats, including low elevation mesotrophic lakes, oligotrophic mountain ponds, and floating sphagnum bogs. The large size and numerous scattered pyrenoids makes this species distinctive and easy to identify.

Closterium moniliferum cells are large and crescent-shaped, with a slightly inflated ventral margin and evenly curved dorsal margin (Figures 3.124–3.127). The apex is bluntly pointed, lacks an apical pore, and contains a well-defined spherical vacuole with many small crystals. The cell wall is colorless or brownish, lacks girdle bands, and usually appears smooth but is very finely striated. Each chloroplast extends nearly to the apex and contains 2–10 (or more) axial pyrenoids. Figure 3.127 shows cells with axial pyrenoids near the apex and scattered pyrenoids near the center of the cell. Cells with this pyrenoid arrangement are often listed as *Closterium moniliferum* var. *submoniliferum* (Woronchin) Krieger; however, Brook and Williamson (2010) state that this feature can be induced in the nominate variety[15] when the cells are grown in high light intensities.

Brook and Williamson (2010) describe *Closterium moniliferum* as a "complex of biological species" that may include more than one morphologically similar species. Not surprisingly, *Closterium moniliferum* it is found in a very wide range of habitats. *Closterium moniliferum* resembles *Closterium ehrenbergii* (Figure 3.74), which is larger and unstriated; and *Closterium leibleinii*, which is smaller, unstriated, and has a tiny subapical pore (Figure 3.102).

Closterium navicula cells are straight and broadly fusiform with truncate apices (Figures 3.128–3.131). The apex is broadly rounded, lacks an apical pore, and contains a spherical vacuole with one or more crystals. The cell wall is colorless, smooth, and lack girdle bands. Each chloroplast extends nearly to the apex and usually contains a single axial pyrenoid (dividing cells may have two pyrenoids).

Nearly all of the northwest Washington *Closterium navicula* specimens were collected in slightly acidic boggy lakes and ponds. Although the cells are typically small, *Closterium navicula* exhibits considerable variation in cell lengths (Figure 3.131). Larger cells may resemble *Closterium closterioides* var. *intermedium* (Figure 3.45), which can be distinguished by its notched chloroplast and (usually) larger size.

Closterium nematodes cells are narrowly crescent-shaped and strongly curved (Figures 3.132–3.135). The apex is narrowly rounded and lacks an apical pore but has a distinctive, thickened, subapical ring. The terminal vacuole is positioned near the top of the chloroplast, below the thickened subapical ring, and contains a single large crystal. The cell wall is brownish and striated, lacks girdle bands, but has prominent sutures between the semi-cells. Each chloroplast extends nearly to the apex and contains 5–8 (or more) axial pyrenoids.

Closterium nematodes is associated with slightly acidic, boggy lakes and ponds. This species resembles *Closterium striolatum* and several other strongly curved species, but none will have the thickened subapical ring.

[15] *Closterium moniliferum* var. *moniliferum*

The ***Closterium parvulum group*** is a poorly defined species complex that needs taxonomic resolution because the cell morphology overlaps with *Closterium dianae* (Figure 3.60), *Closterium incurvum* (Figure 3.85), *Closterium leibleinii* (Figure 3.102), *Closterium parvulum* (Figure 3.136), and *Closterium venus* (Figure 3.182). All members of this group have strongly and evenly curved, crescent-shaped cells with an acutely rounded apex. The cells should have an indistinct pore located just below the apex (subapical) on the dorsal margin, but this feature is not always visible. In addition to the group characteristics described above, the species ***Closterium parvulum*** is characterized by a thickened apex wall and large, poorly defined terminal vacuole that occupies the space between the top of the chloroplast and the apex (Figures 3.136–3.143). The vacuole contains 2–8 (or more) crystals that are distributed throughout the large vacuole. The cell wall is colorless or yellowish brown, unstriated, and lacks girdle bands. Each chloroplast contains 2–6 (or more) axial pyrenoids and extends nearly to the apex, ending just below the large terminal vacuoles

Figures 3.139–3.143 appear to represent three different varieties, forms, or species within the *Closterium parvulum* species complex, all with features that differ from the *Closterium parvulum* specimens depicted in Figures 3.136–3.138. The specimens in Figures 3.139–3.141 (*Closterium parvulum* group var. A) have nearly all of the features for this group, including the thickened apex wall and small subapical pore on the dorsal margin, but are much larger than any of the varieties listed by Prescott et al. (1975). The specimens in Figures 3.142–3.143 (*Closterium* cf. *parvulum* var. B) have a single large crystal in the terminal vacuole and are strongly curved, resembling *Closterium incurvum* (Figure 3.85), except in size.

Closterium praelongum cells are narrowly cylindrical, with nearly parallel sides and almost no curvature until near the apex, where the cell becomes tapered and gently curved (Figures 3.144–3.147). The apex is truncated and somewhat narrowed, with the ventral margin narrowing abruptly and the dorsal margin turning slightly outward (recurved). The apex may have an apical pore, but this feature is not always visible. The spherical terminal vacuole contains one or more crystals that may form stacked groups. The cell wall is colorless or brownish, finely striated, and lacks true girdle bands but may have asymmetric false girdle bands. Each chloroplast extends nearly to the apex and contains 7-25 axial pyrenoids.

Closterium praelongum can be found in a wide range of habitats, including eutrophic waters. Most of the northwest Washington specimens were collected from residential ponds and ditches, but a few samples were collected along shorelines in slightly acidic, mesotrophic lakes. *Closterium praelongum* is very similar in size and shape to *Closterium lineatum* (Figure 3.112), which lacks the recurved apex. *Closterium lineatum* also resembles *Closterium gracile* (Figure 3.78), which can be distinguished by its smooth, unstriated cell wall and *Closterium juncidum* (Figure 3.112), which is much smaller and is more likely to be collected in boggy, slightly acidic sites.

Closterium pritchardianum cells are narrowly cylindrical, with nearly parallel sides in the mid-region (Figures 3.148–3.149). The dorsal margin is slightly but evenly curved; the ventral margin is usually less curved, and may be straight in the mid-region of the cell. The apex is lacks a pore and is truncated, often appearing to be recurved because it is abruptly narrowed on the dorsal side. The terminal vacuole is spherical and contains many small crystals. The cell wall is colorless, yellowish, or light brown; lacks girdle bands; and is striated with single vertical rows of punctae. Each chloroplast extends nearly to the apex and contains five or more axial pyrenoids.

Closterium pritchardianum is found in boggy, slightly acidic lakes and ponds. This species resembles *Closterium acerosum* (Figure 3.10), which lacks the distinctive double rows of punctae; and *Closterium braunii* (Figure 3.38), which is striated with double rows of closely spaced punctae. Very careful examination is needed to distinguish *Closterium pritchardianum* from the other two species. Habitat is occasionally helpful because *Closterium acerosum* is more likely to be present in eutrophic and polluted habitats, but *Closterium acerosum* can also be collected in acidic or boggy ponds.

Closterium pronum cells are narrowly fusiform and straight or nearly straight, often with some curvature near the apex (Figures 3.150–3.152). The sides are tapered across most of the length of the cell except for near the center, which has parallel sides. The terminal vacuole is long and poorly defined, lacks an apical pore, and contains one or more small crystals that often form small bead-like chains. The cell wall is colorless, smooth, and lacks girdle bands. Each chloroplast has 5–12 axial pyrenoids and stops well below the apex.

Closterium pronum is usually found in slightly acidic, boggy lakes and ponds. It resembles *Closterium aciculare* (Figure 3.16), which is much longer, has an apical pore (hard to see), and parallel sides along most of the length of the cell; and *Closterium acutum* (Figure 3.19), which is usually shorter, with a chloroplast that extends nearly to the apex of the cell.

Closterium pseudolunula cells are large and broadly fusiform or crescent-shaped, with a nearly straight or slightly inflated ventral margin and slightly curved dorsal margin (Figures 3.153–3.155). The apex is bluntly truncated and may appear recurved due to the uneven dorsal/ventral curvature. The terminal vacuole is spherical, lacks an apical pore, and contains many small crystals. The cell wall is colorless or brownish, lacks girdle bands, and may appear smooth, but is actually very finely striated. Each chloroplast extends nearly to the apex and contains 4–10 large axial pyrenoids. *Closterium pseudolunula* closely resembles *Closterium lunula* (Figure 3.119), but *Closterium lunula* has many small scattered pyrenoids (not axial) and is usually larger. *Closterium pseudolunula* also resembles *Closterium acerosum* (Figure 3.10), which is narrower relative to length (L/W usually >10). *Closterium pseudolunula* was collected in a very broad range of habitats, including low elevation mesotrophic lakes, oligotrophic mountain ponds, and floating sphagnum bogs.

Closterium pusillum cells are very small, irregularly cylindrical, with a straight or nearly straight ventral margin and very slightly curved dorsal margin (Figures 3.156–3.159). The apex is broadly rounded and nearly as wide as the rest of the cell; apical pores are absent. The terminal vacuole usually contains one large crystal but occasionally has several smaller fused crystals. The cell wall is colorless, smooth, and lacks girdle bands. Each chloroplast contains 1–2 axial pyrenoids and extends to the base of a large, spherical terminal vacuole. *Closterium pusillum* is morphologically variable, and because of its small size, it is easy to overlook in a sample. The northwest Washington specimens were collected along the shoreline in slightly acidic, oligo-mesotrophic lakes.

Closterium ralfsii cells are large and crescent-shaped or fusiform, with a slightly to moderately curved dorsal margin and inflated ventral margin (Figures 3.160–3.164). The apex is truncated at an angle and contains a large apical pore. The spherical terminal vacuoles contain one or more crystals; when many crystals are present they may form fused groups. The cell wall is yellowish to dark reddish brown, lacks girdle bands, and is finely striated, with tiny punctae between the striations. The striations stop short of the apex, but the punctae continue to the apex, making this feature difficult to see, especially in darkly colored cells. Each chloroplast extends nearly to the apex and contains 4–10 (or more) axial pyrenoids. All of the northwest Washington specimens appear to be ***Closterium ralfsii* var. *hybridum***, which is narrower, with a less pronounced ventral inflation, and with finer striations compared to the nominate variety.[16]

[16] *Closterium ralfsii* var. *ralfsii*

Closterium ralfsii var. *hybridum* is found in slightly acidic, boggy lakes and ponds. This species can be difficult to separate from some varieties of *Closterium striolatum* (Figure 3.178), which are usually smaller, lack the ventral inflation, have girdle bands, and usually have a single large apical crystal.

Closterium* cf. *rectimarginatum cells are fusiform and nearly straight except near the apex, which is slightly curved along the dorsal margin (Figures 3.165–3.168). The apex in the northwest Washington specimens is truncated or broadly rounded,[17] lacks an apical pore, and has an oval or spherical vacuole with several large crystals. The cell wall is colorless, smooth, and lacks girdle bands. Each chloroplast extends almost to the apex and contains 2–8 axial pyrenoids. *Closterium rectimarginatum* appears to be a rare desmid because it is not described in most desmid keys, so the species identification is uncertain. The northwest Washington specimens were collected from several slightly acidic, mesotrophic ponds and lakes.

Closterium rostratum cells are bow-shaped, with a broadly inflated center, and short, curved, beak-like extensions (Figures 3.169–3.173). The dorsal margin is usually more strongly curved than the ventral margin, which can be nearly straight in the central portion of the cell. The apex is slightly inflated and contains a small apical pore. The vacuoles are located at the upper end of each chloroplast near the base of the beak-like extensions (subapical), and contain several small crystals. The cell wall ranges from colorless to yellowish brown, lacks girdle bands, and is faintly striated. The chloroplasts are confined to the central fusiform portion of the cell, and each contains 3–8 axial pyrenoids.

Closterium rostratum is usually found in slightly acidic, mesotrophic lakes and ponds, but the northwest Washington specimens were collected in a wide variety of habitats, including moderately eutrophic residential ponds. *Closterium rostratum* cells exhibit considerable morphological variability, even in samples collected at the same location (Figure 3.173). *Closterium rostratum* resembles *Closterium kuetzingii* (Figure 3.97) and *Closterium setaceum* (Figure 3.174), both of which are much more delicate in structure have have long, mostly straight extensions. The *Closterium rostratum* extensions form a continuous curve with the fusiform portion of the cell along the dorsal margin of the cell.

Closterium setaceum cells are bow-shaped and nearly straight, with a narrowly inflated center, and long, narrow, beak-like extensions (Figures 3.174–3.177). The extensions are straight almost to the apex, then gently curved, giving the cell a

[17] Scott and Prescott (1961) describe the *Closterium rectimarginatum* apex as narrowly rounded.

symmetric appearance with equal dorsal and ventral curvature. Each extension is longer than the combined length of both chloroplasts. The apex is usually slightly expanded and contains a small apical pore. The vacuoles are located at the upper end of each chloroplast near the base of the narrow extensions (subapical), and contain several small crystals. The cell wall is colorless or pale yellow, lacks girdle bands, and is faintly striated; the striations are very fine, so the cell wall usually appears smooth. The chloroplasts are confined to the central fusiform portion of the cell and each contains 2–3 axial pyrenoids.

Closterium setaceum is usually found in slightly acidic, oligo-mesotrophic or mesotrophic lakes and ponds. *Closterium setaceum* can be difficult to distinguish from *Closterium kuetzingii* (Figure 3.97), especially because both species may be present in the same sample. The best separation feature is the greater length of the extensions in *Closterium setaceum*, which gives the species a more delicate appearance (see Figure 3.101).

Closterium striolatum cells are approximately cylindrical, with a nearly straight center and slightly curved upper region (Figures 3.178–3.181). The center of the cell may have parallel sides or may be slightly inflated above the isthmus; the upper portion of the cell is gently curved and tapered to the apex. The apex is broadly truncated (sometimes rounded or inflated), with an apical pore. The terminal vacuole is spherical and contains one or more aggregated crystals. The cell wall is brown or rusty colored, distinctly striated, with girdle bands, and sutures. Each chloroplast extends nearly to the apex and contains 4–10 (or more) axial pyrenoids.

Closterium striolatum is common in boggy, slightly acidic lakes and ponds, but can also be found in other habitats, including eutrophic residential sites. The species is polymorphic, but the heavily striated, brownish cell wall is fairly distinctive. *Closterium striolatum* resembles *Closterium costatum* (Figure 3.51), which has much wider cells; *Closterium nematodes* (Figure 3.132), which has a thickened subapical ring; and *Closterium ralfsii* (Figure 3.160), which has an inflated ventral margin, lacks girdle bands, and has many small crystals in the terminal vacuole.

Closterium venus cells are relatively small, crescent-shaped, and strongly curved ($\sim$150–160°; Figures 3.182–3.184). The ventral margin is evenly curved, with no median inflation. The apex is acute, with a small pore just below the apex on the dorsal side. The terminal vacuole is well-defined and contains one or more large crystals. The cell wall is colorless or yellowish brown, smooth, and lacks girdle bands. The chloroplasts usually only fills about half of the cell, ending well below the apex; each chloroplast contains 1–3 large, axial pyrenoids.

Closterium venus cells are very similar to *Closterium incurvum* (Figure 3.85). Both species are characterized by strongly curved, crescent-shaped cells with nearly the same size ranges for length and width. Both species can be present at the same site (Figure 3.88; Sovran, et al., 2013), so habitat does not help with separation. Despite the morphological similarity of the vegetative cells, the separation between *Closterium venus* and *Closterium incurvum* is supported by differences in their zygotes (Cook, 1963). The best visual features for separating these two species is the dorsal curvature, which is nearly hemispherical for *Closterium incurvum* vs. crescent-shaped for *Closterium venus*; and the chloroplast length, which extends nearly to the apex in *Closterium incurvum* cells, but ends well below the apex in *Closterium venus* cells.

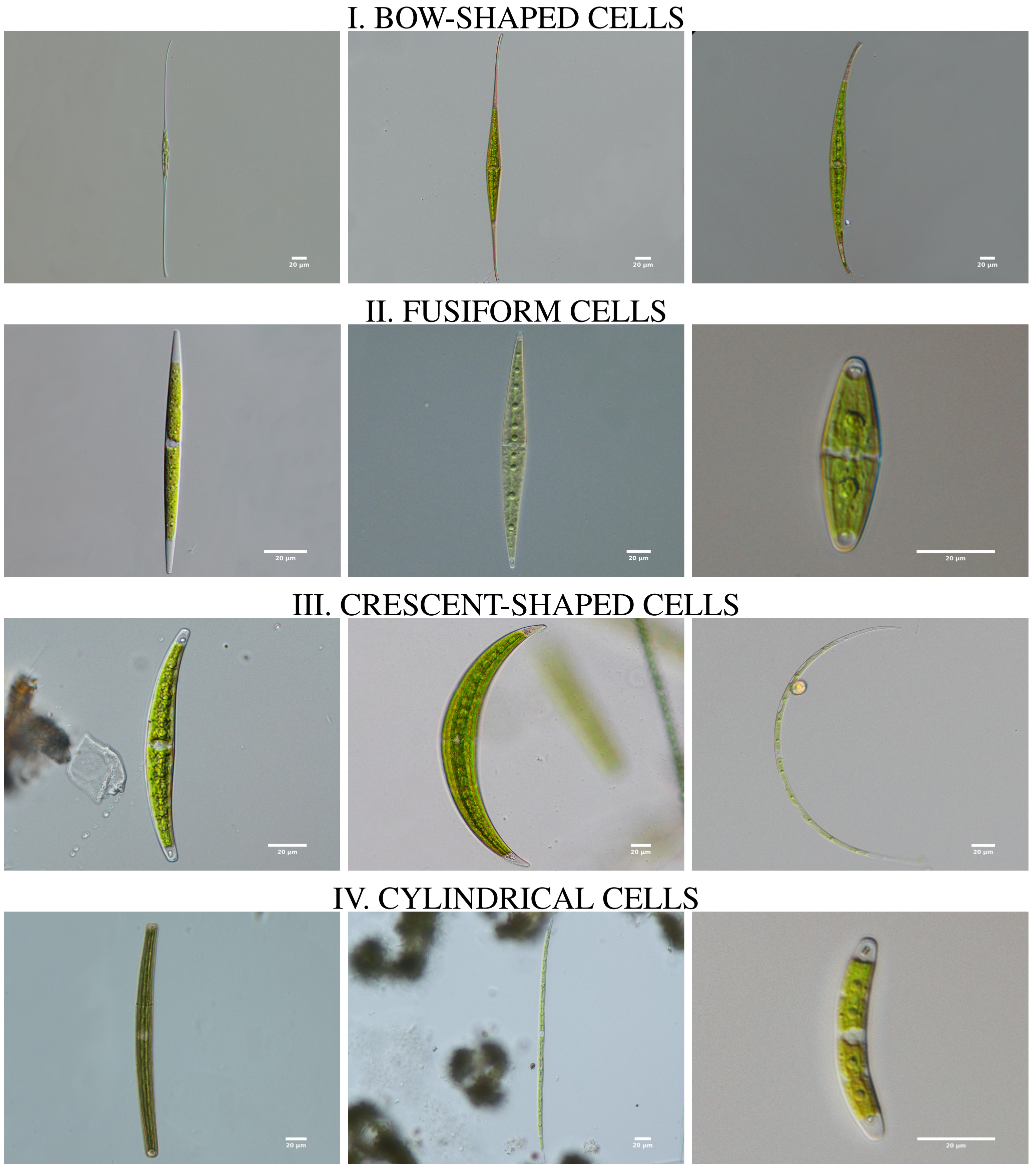


Figure 3.1: Examples of *Closterium* cell shapes. First row: bow-shaped cells with fusiform center and beak-like apical extensions (from left to right, *Closterium setaceum*, *Closterium kuetzingii*, *Closterium rostratum*). Second row: fusiform cells that are expanded at the center and evenly tapered to the apex (from left to right, *Closterium* cf. *cornu*, *Closterium* cf. *rectimarginatum*, *Closterium navicula*). Third row: crescent-shaped cells that are curved on one or both margins, usually with greater curvature on dorsal margin, and tapered near the apex (from left to right, *Closterium littorale*, *Closterium* cf. *parvulum*, *Closterium acutum* var. *variable*). Fourth row: cylindrical cells with parallel sides near center; cells are often curved and may be tapered near apex (from left to right, *Closterium directum*, *Closterium limneticum*, *Closterium pusillum*).

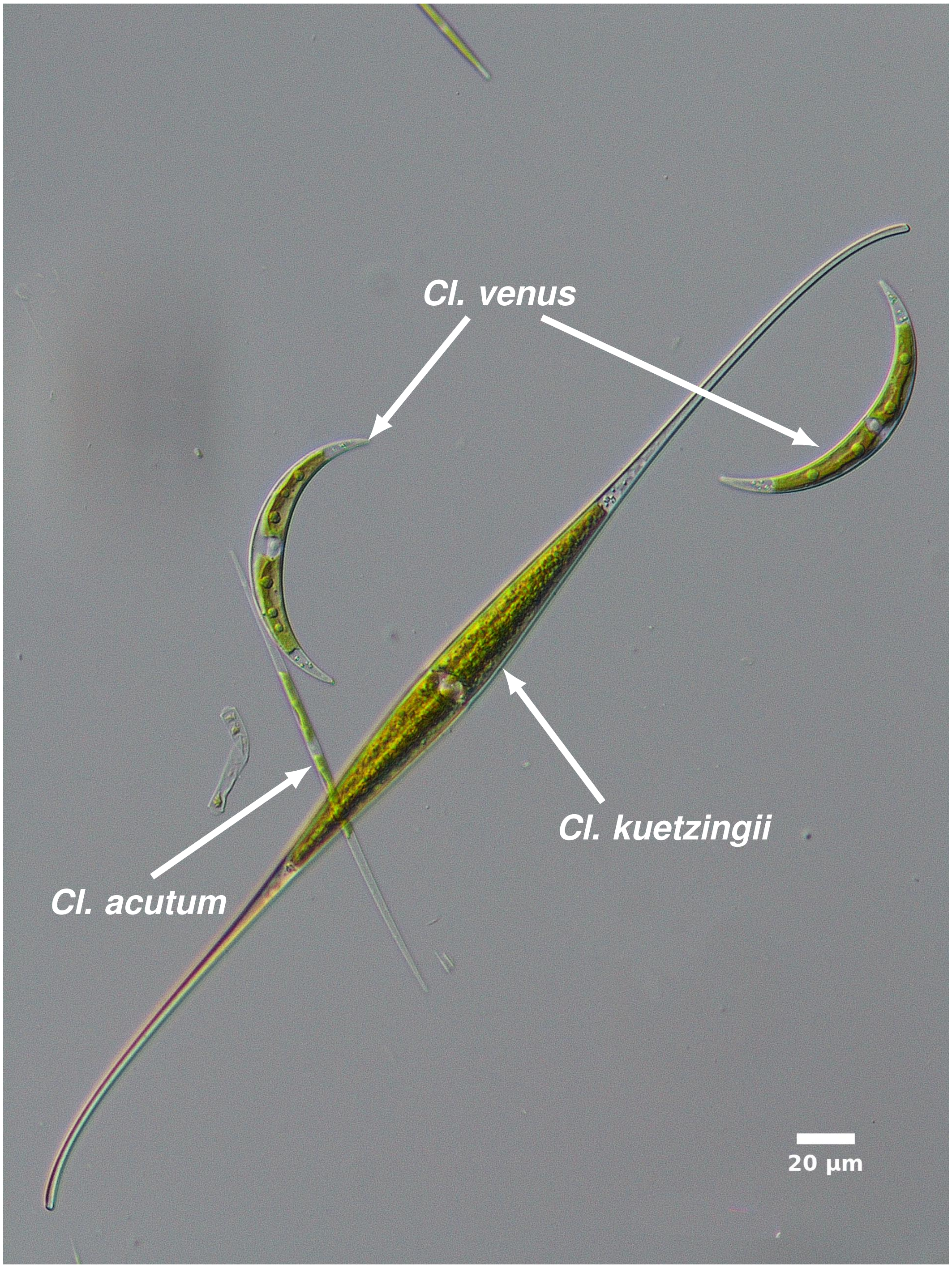


Figure 3.2: Size and curvature variations between three species of *Closterium*.

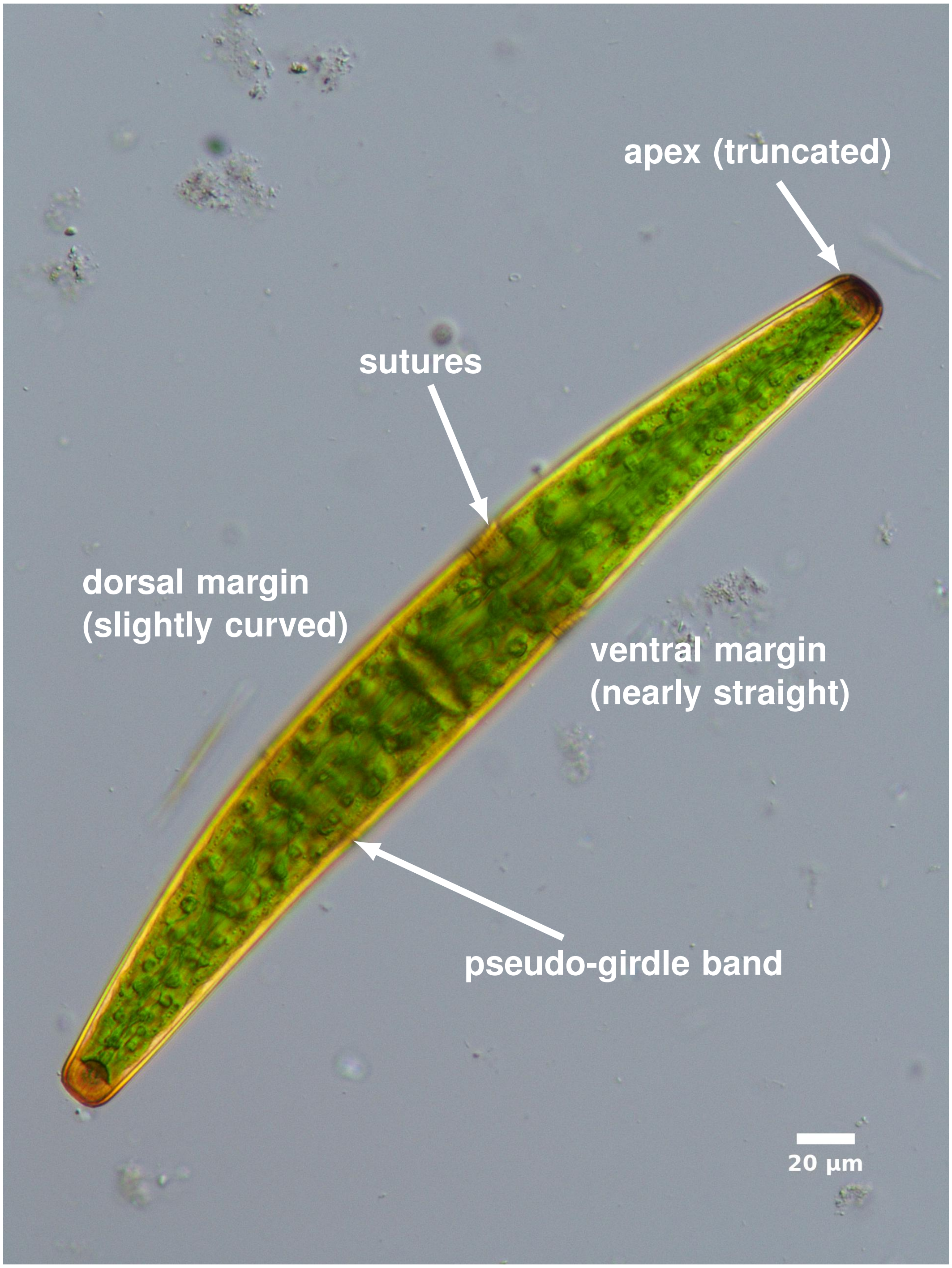


Figure 3.3: *Closterium* basic morphological features (*Closterium baillyanum*).

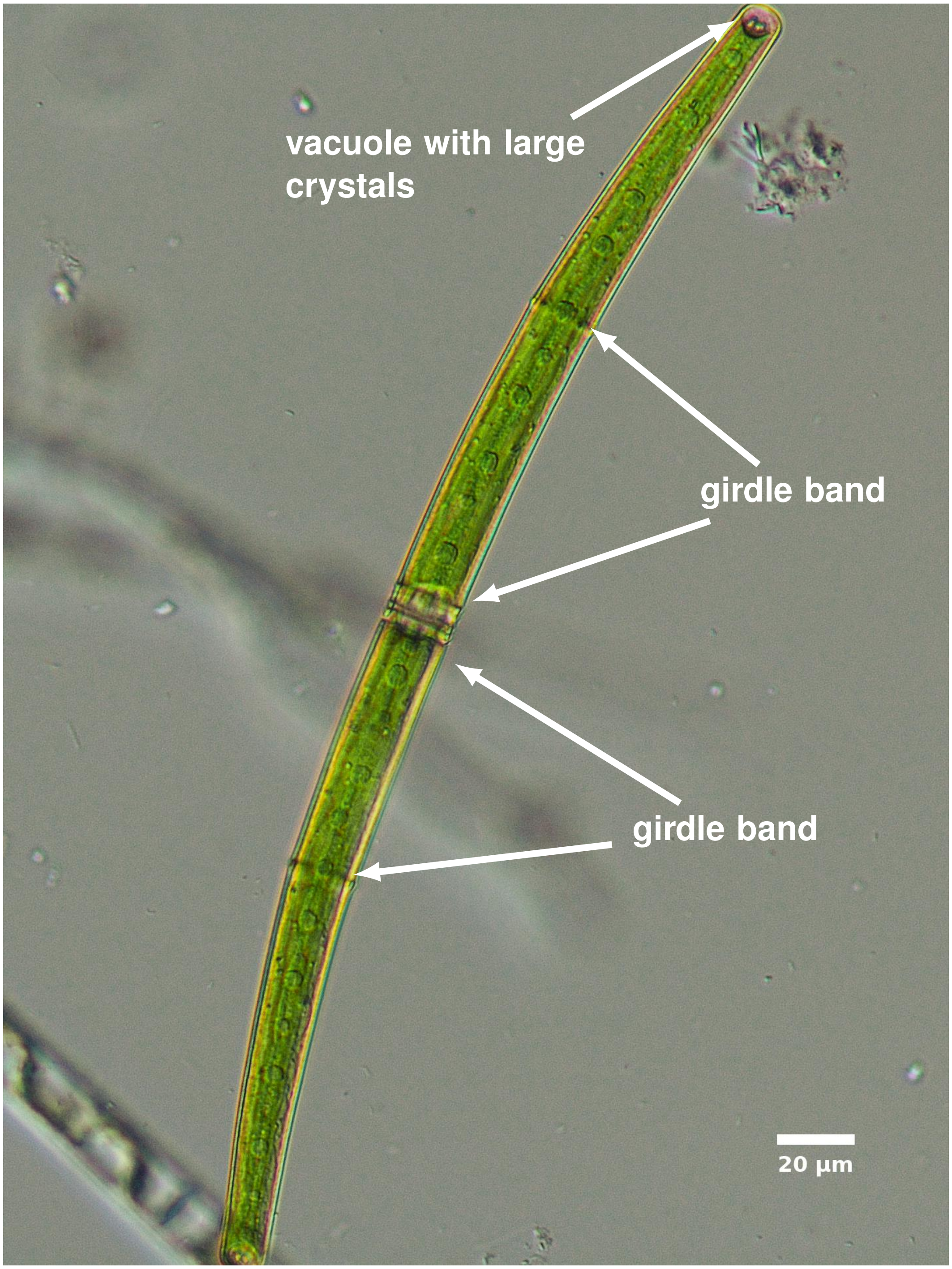


Figure 3.4: Example of *Closterium* girdle bands and terminal vacuole (*Closterium directum*).

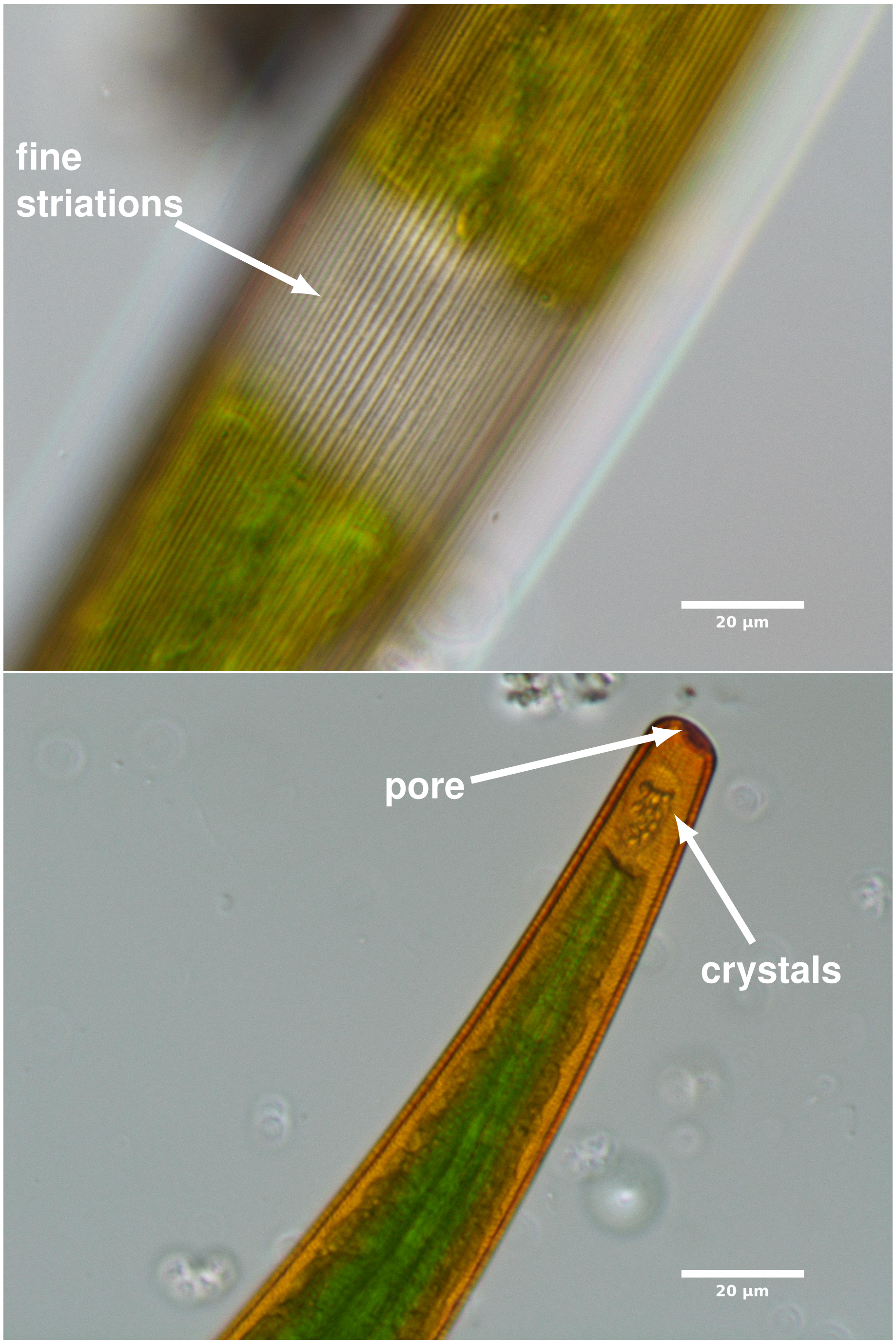
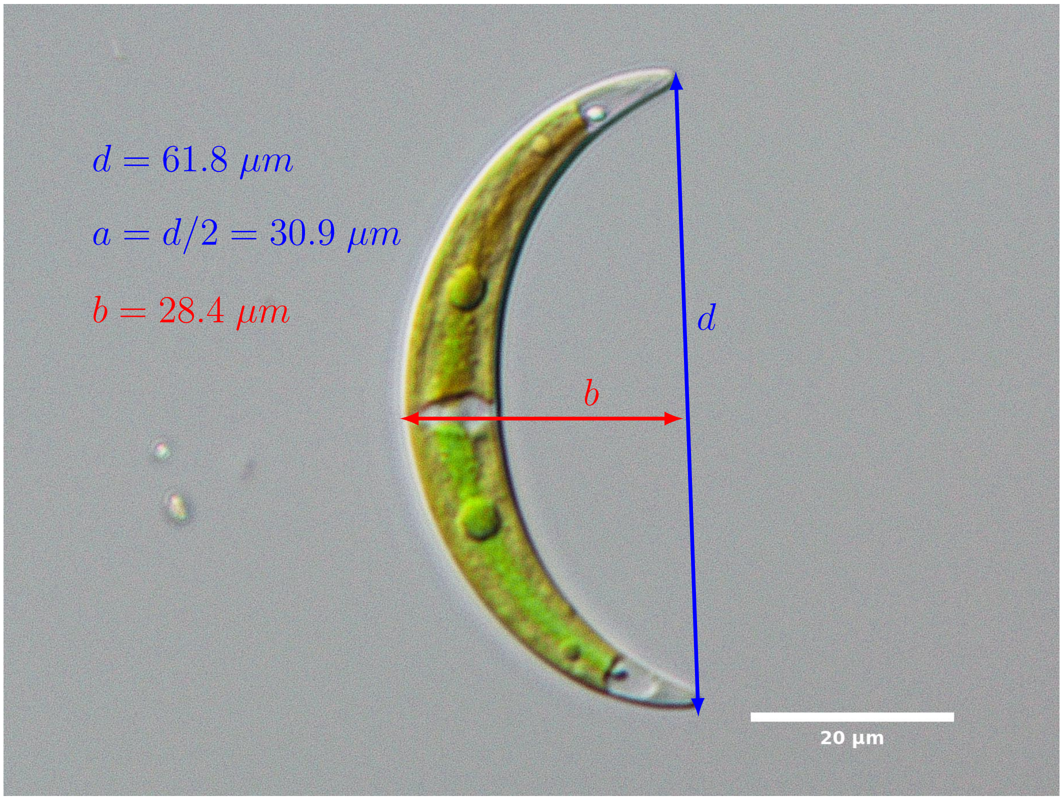


Figure 3.5: Example of *Closterium* wall striations, apical crystals, and apical pore (*Closterium ralfsii*).



$$\text{curvature} = 2\sin^{-1}\left(\frac{2ab}{a^2+b^2}\right) \times \frac{180}{\pi}$$

$$\text{curvature} = 2\sin^{-1}\left(\frac{2 \times 30.9 \times 28.4}{30.9^2+28.4^2}\right) \times \frac{180}{\pi} = 170^\circ \text{ (strongly curved)}$$

Figure 3.6: Example of cell curvature measurements.

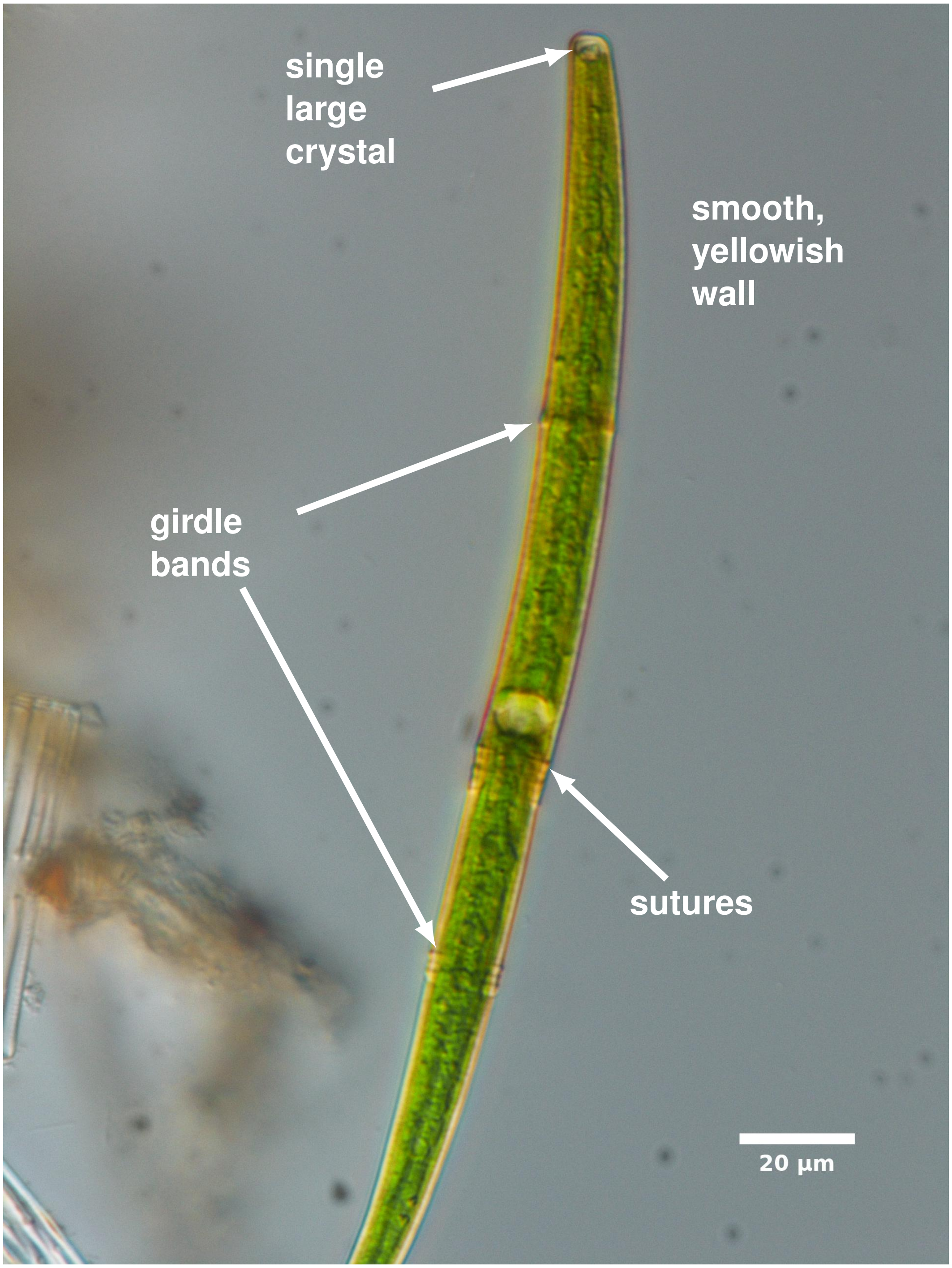


Figure 3.7: *Closterium abruptum* (DIC), small pond on trail to Big Four Ice Caves, Mountain Loop Highway, Snohomish County.

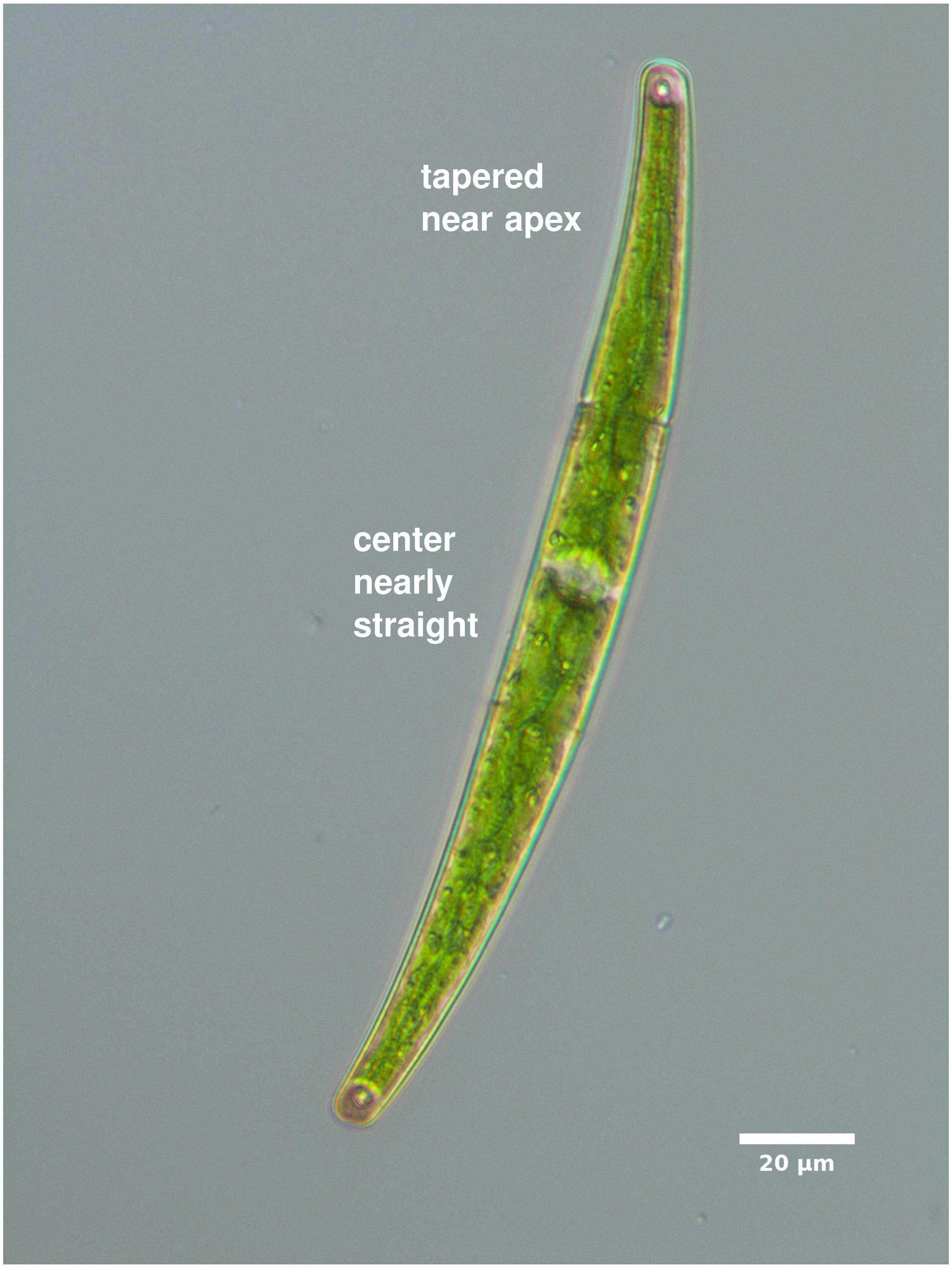


Figure 3.8: *Closterium abruptum* (DIC), Lower Ashland Lake, Mountain Loop Highway, Snohomish County.

Figure 3.9: *Closterium abruptum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

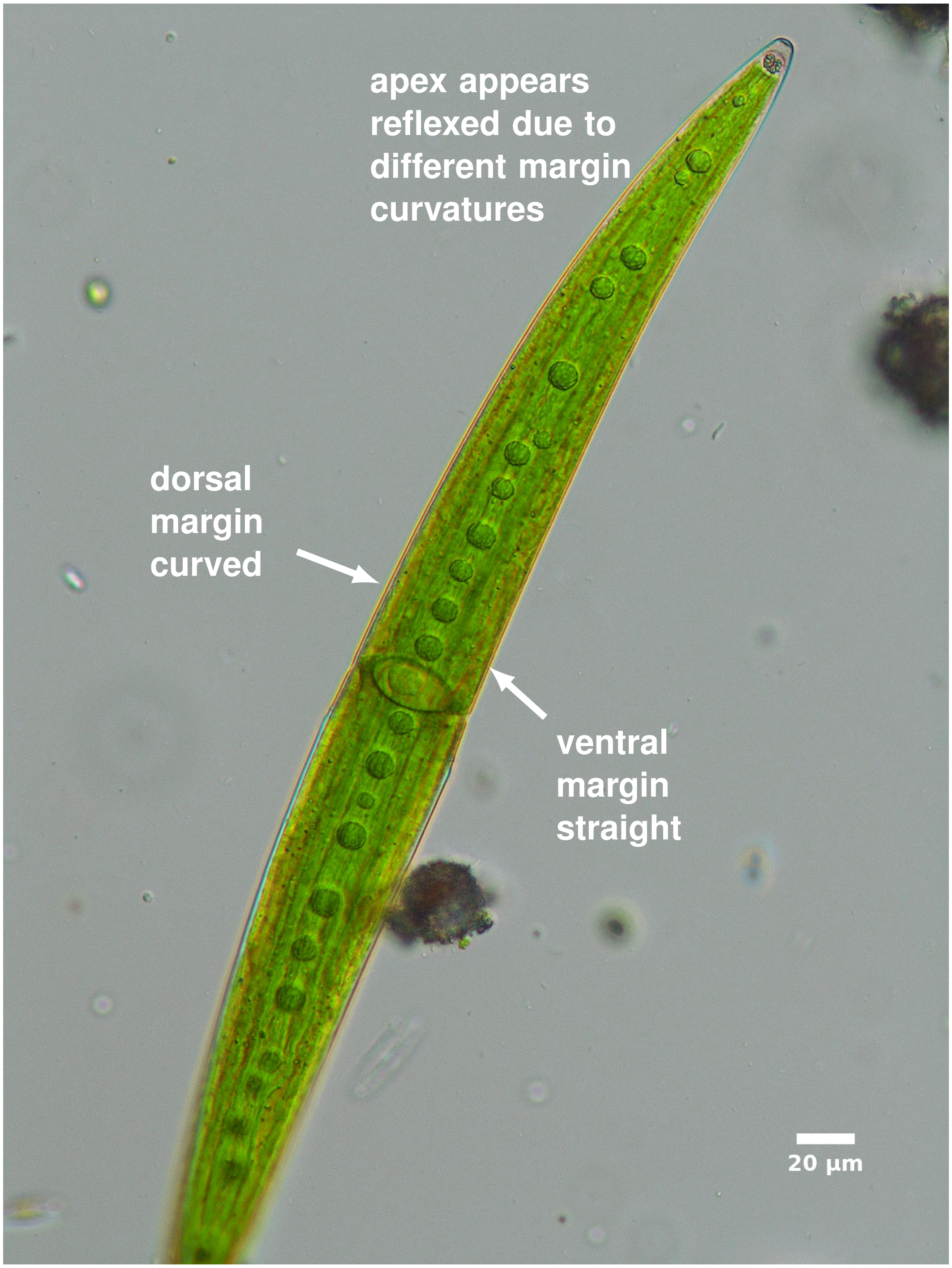


Figure 3.10: *Closterium acerosum* (DIC), small residential pond, Whatcom County.

Figure 3.11: *Closterium acerosum* (DIC), Western Washington University storm water treatment pond, Whatcom County.

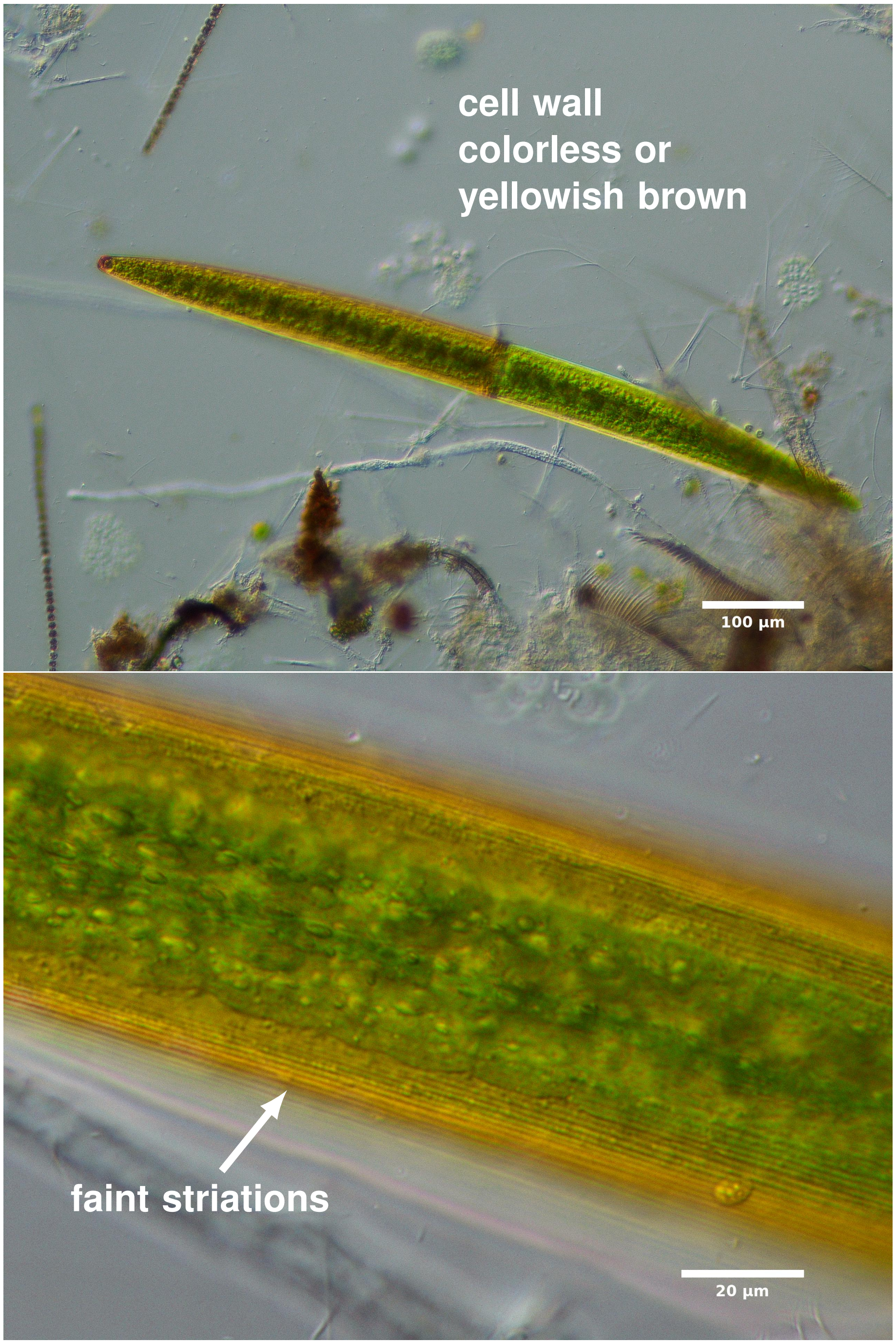


Figure 3.12: *Closterium acerosum* (DIC/DIC), Clear Lake, Skagit County (upper/lower images).

Figure 3.13: *Closterium acerosum* var. *elongatum* apex (bright field), Beaver Lake, Skagit County.

Figure 3.14: *Closterium acerosum* var. *elongatum* (DIC), Beaver Lake, Skagit County.

Figure 3.15: *Closterium acerosum* var. *elongatum* apex (DIC), Beaver Lake, Skagit County.

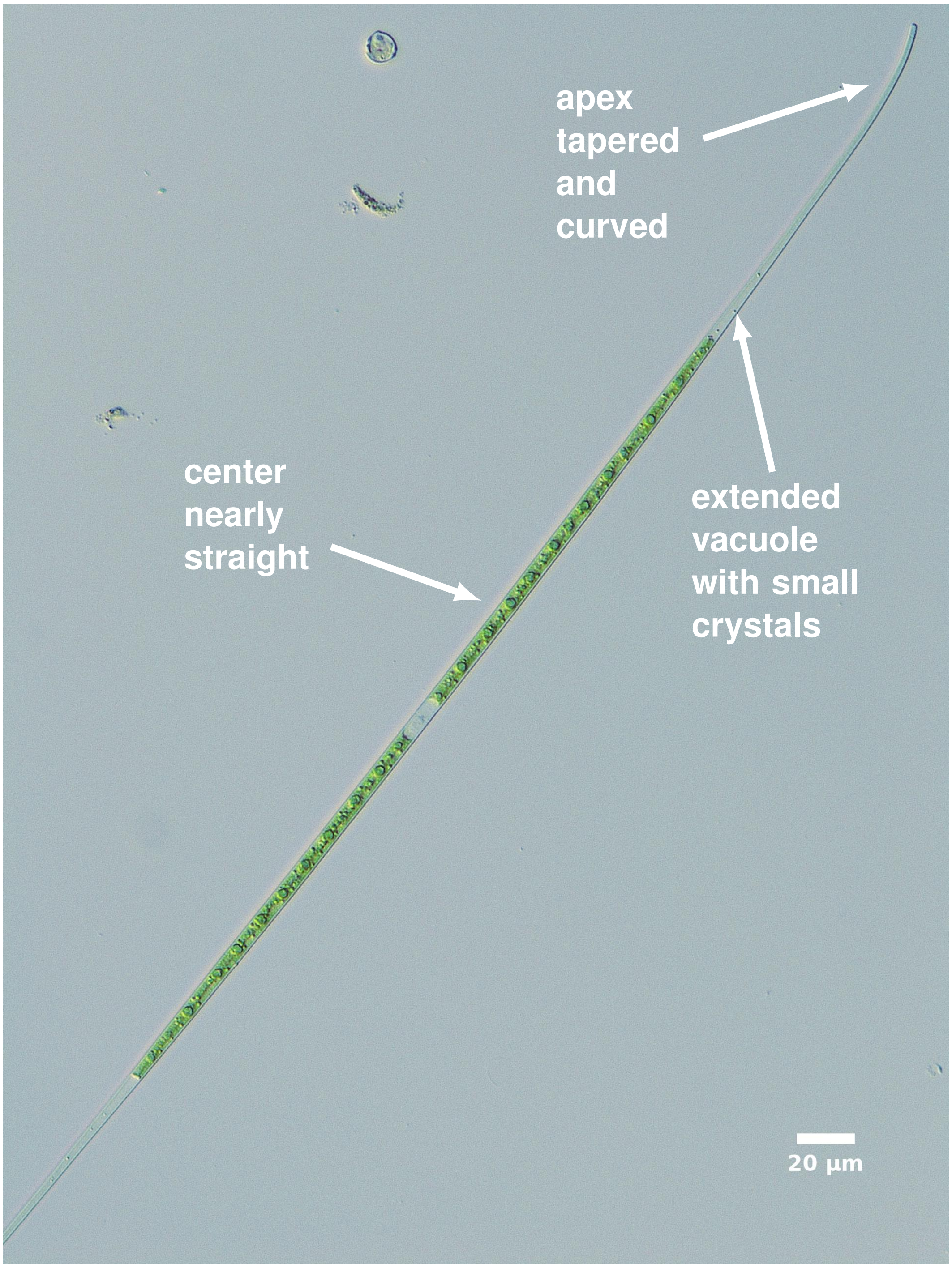


Figure 3.16: *Closterium aciculare* (DIC), Lake Terrell, Whatcom County.

Figure 3.17: *Closterium aciculare* (DIC), Lake Terrell, Whatcom County.

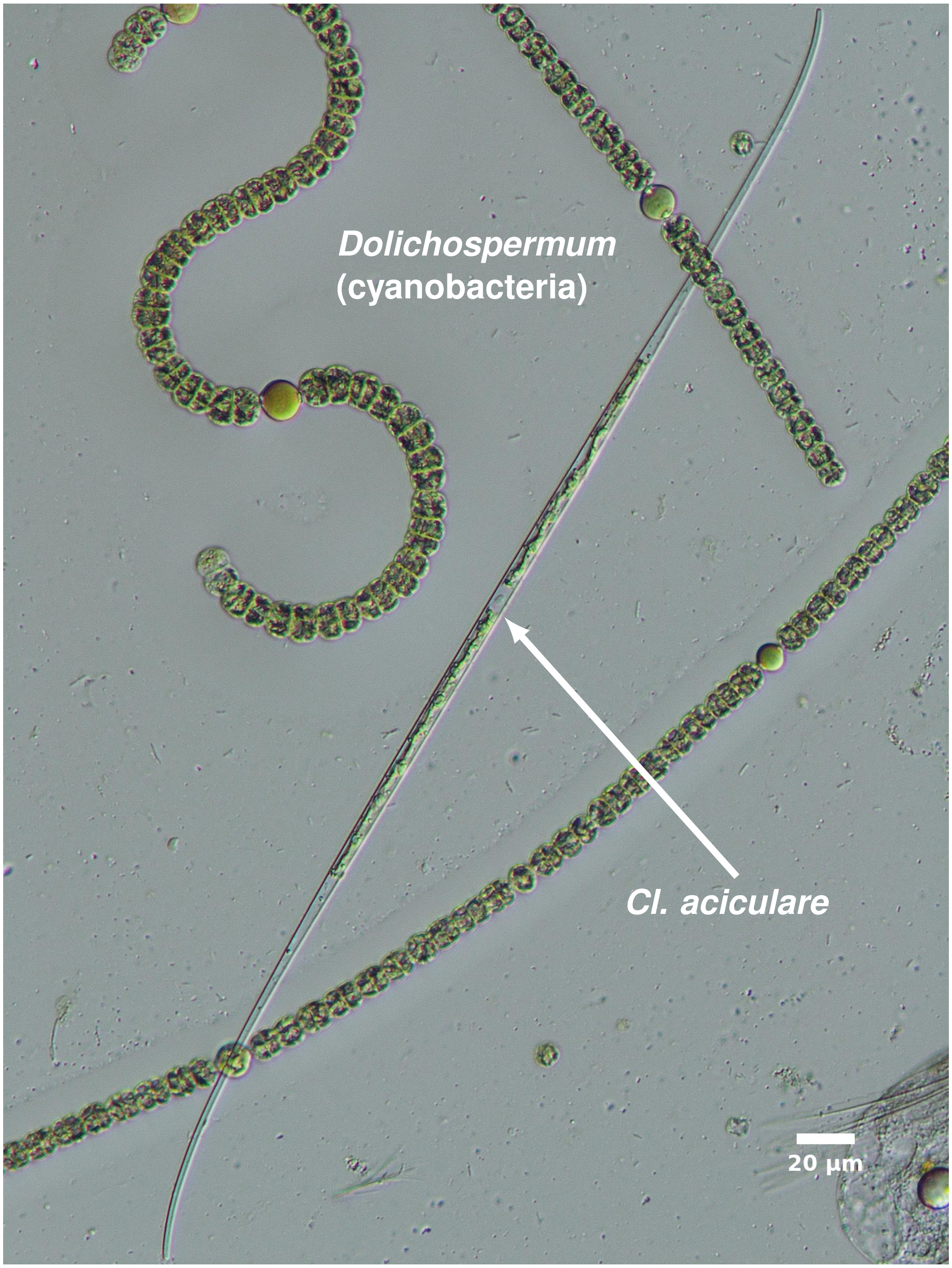


Figure 3.18: *Closterium aciculare* in cyanobacteria bloom (DIC), Heart Lake, Skagit County.

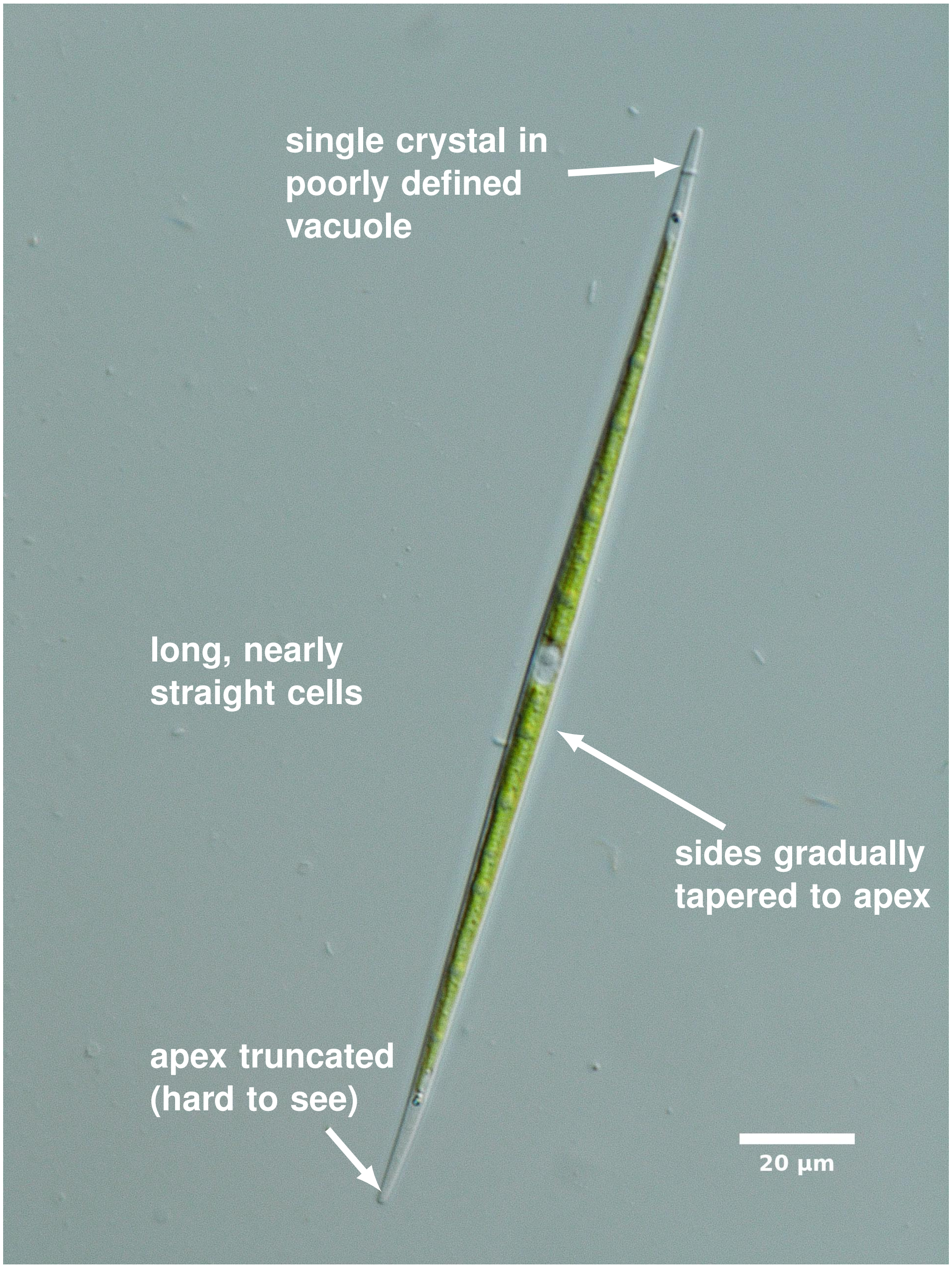


Figure 3.19: *Closterium acutum* (DIC), Reed Lake, Whatcom County.

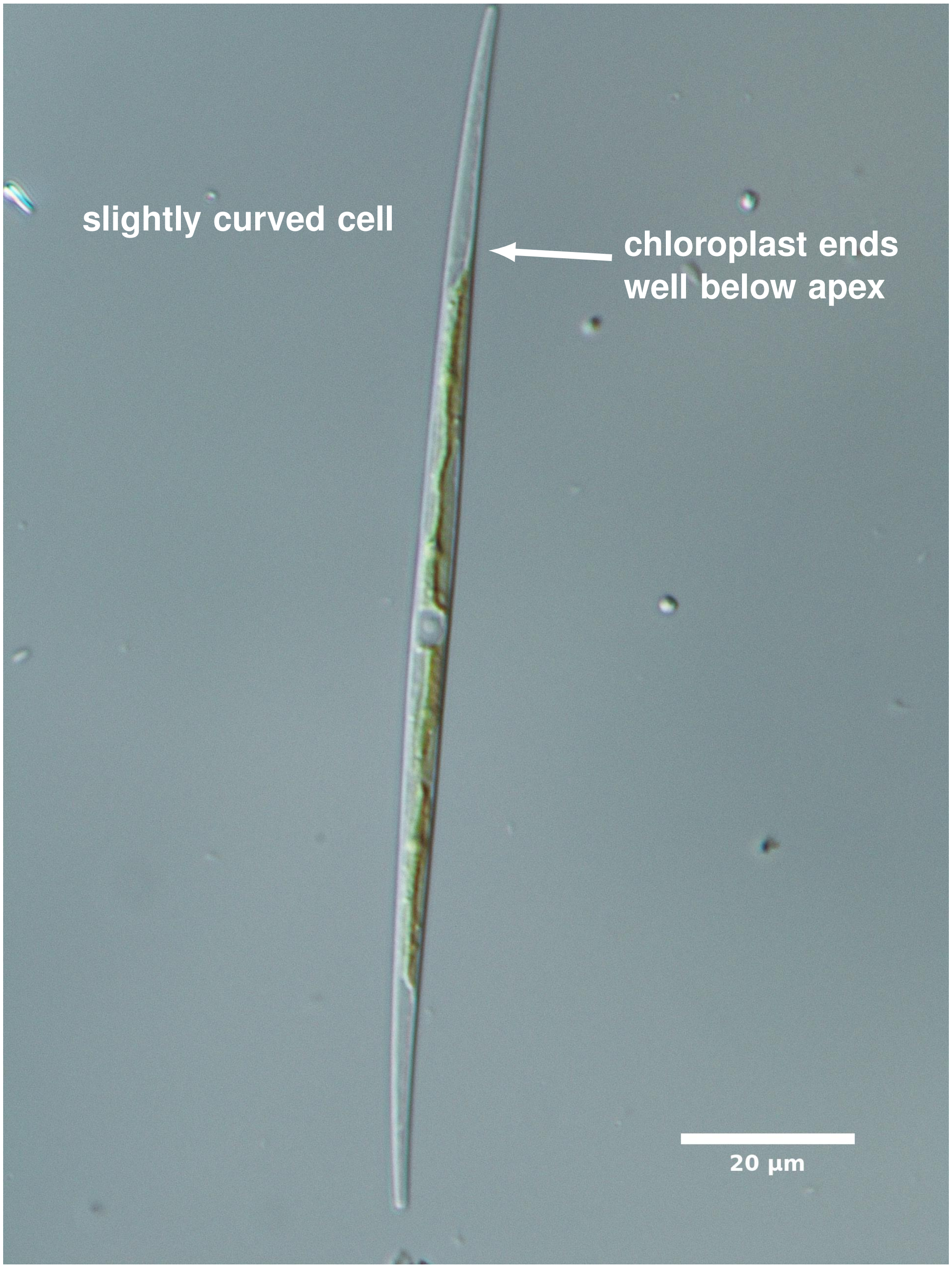


Figure 3.20: *Closterium acutum* (DIC), small pond on trail to Dock Butte, Mt. Baker area, Skagit County.

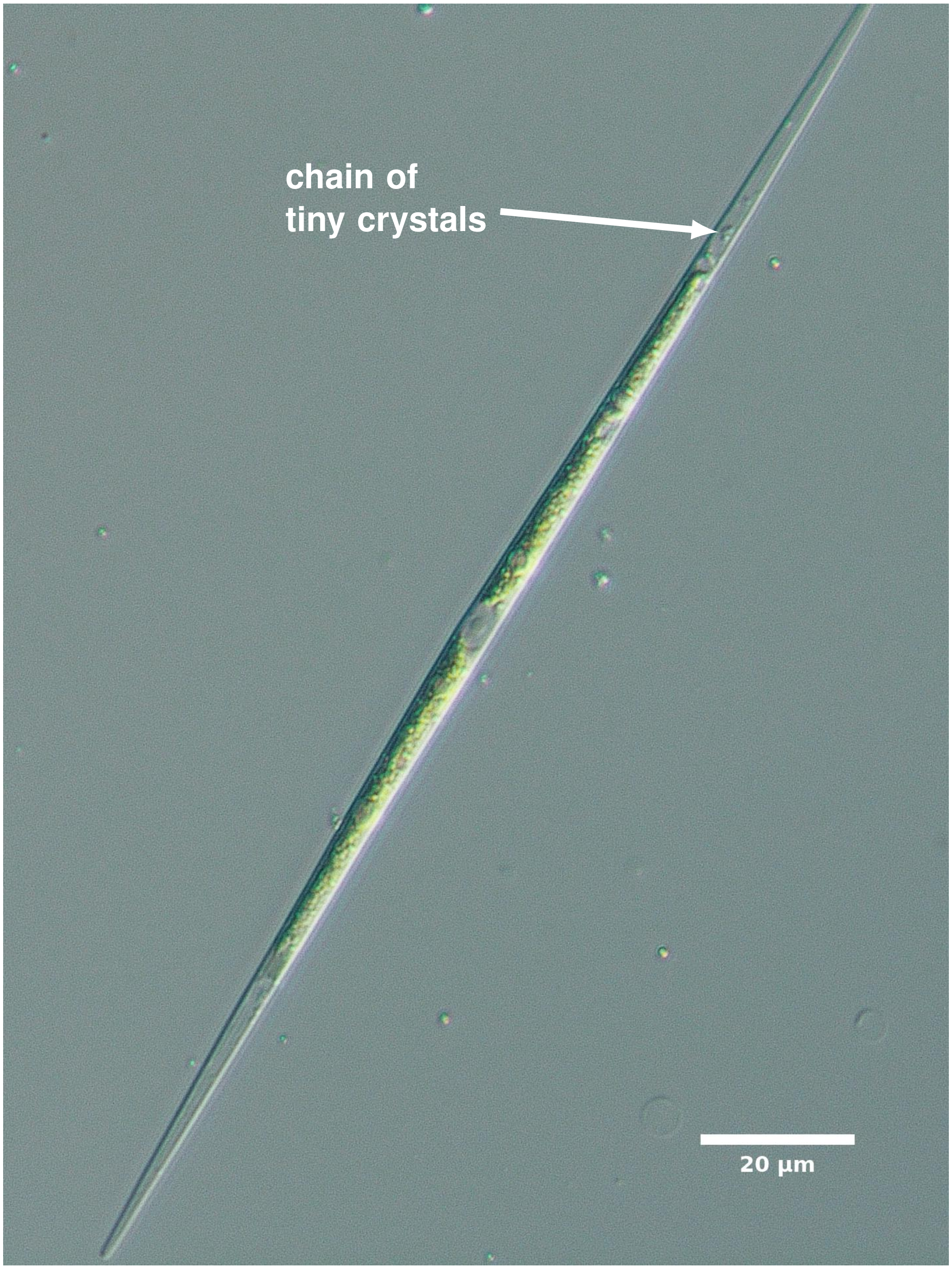


Figure 3.21: *Closterium acutum* (DIC), Lake Terrell, Whatcom County.

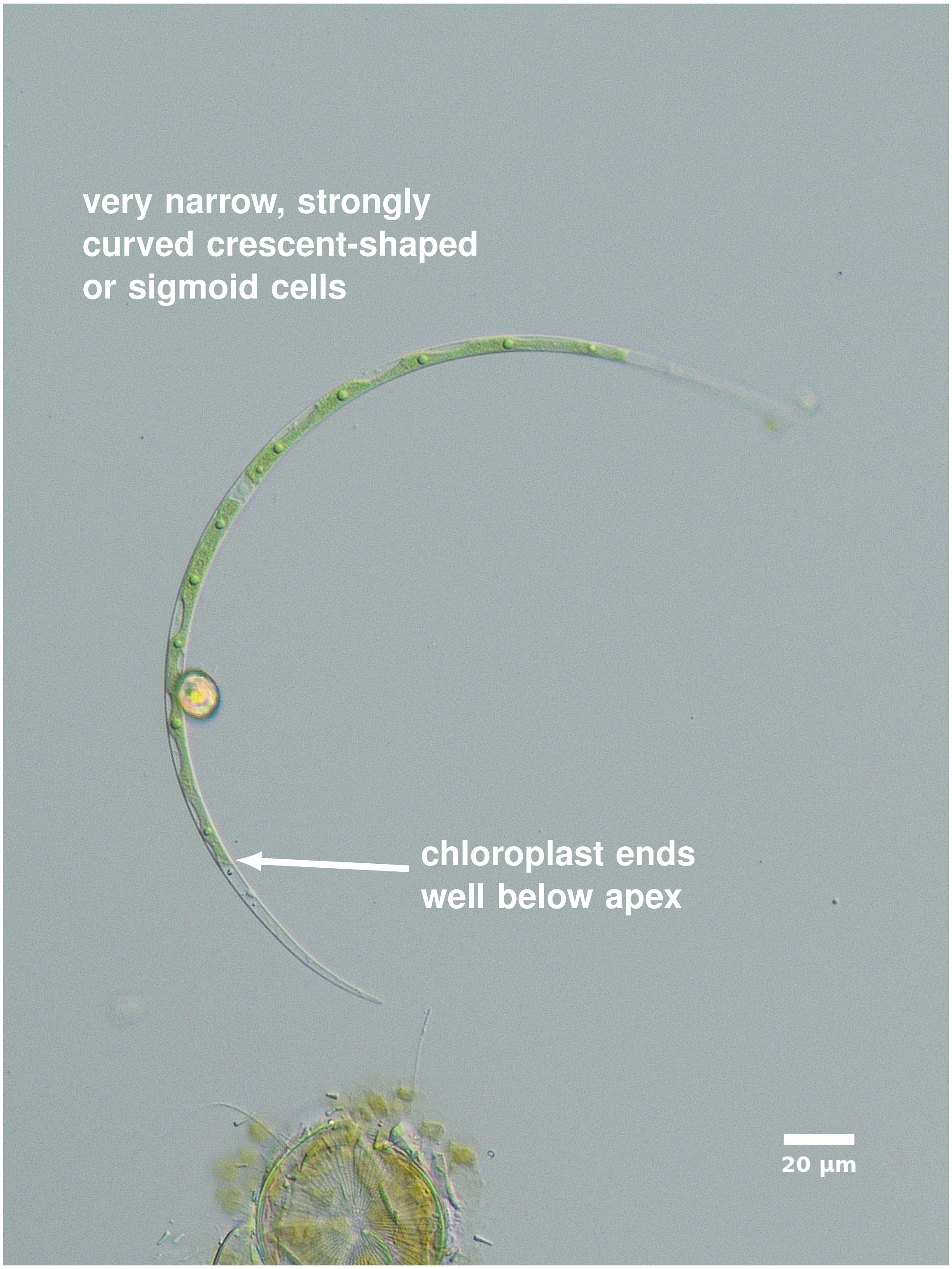


Figure 3.22: *Closterium acutum* var. *variable* (DIC), Moses Lake (eastern Washington), Grant County.

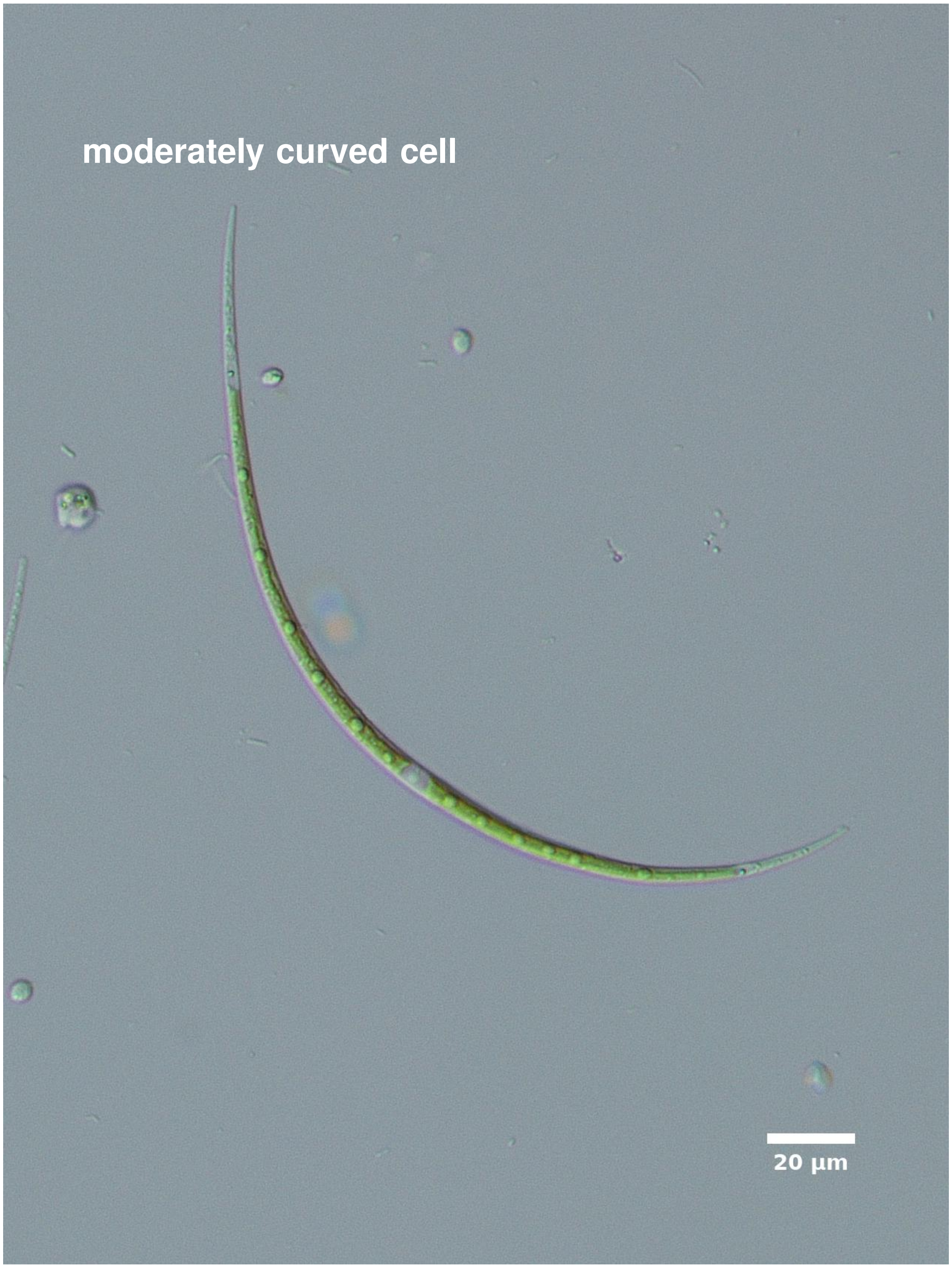


Figure 3.23: *Closterium acutum* var. *variable* (DIC), Heart Lake, Skagit County.

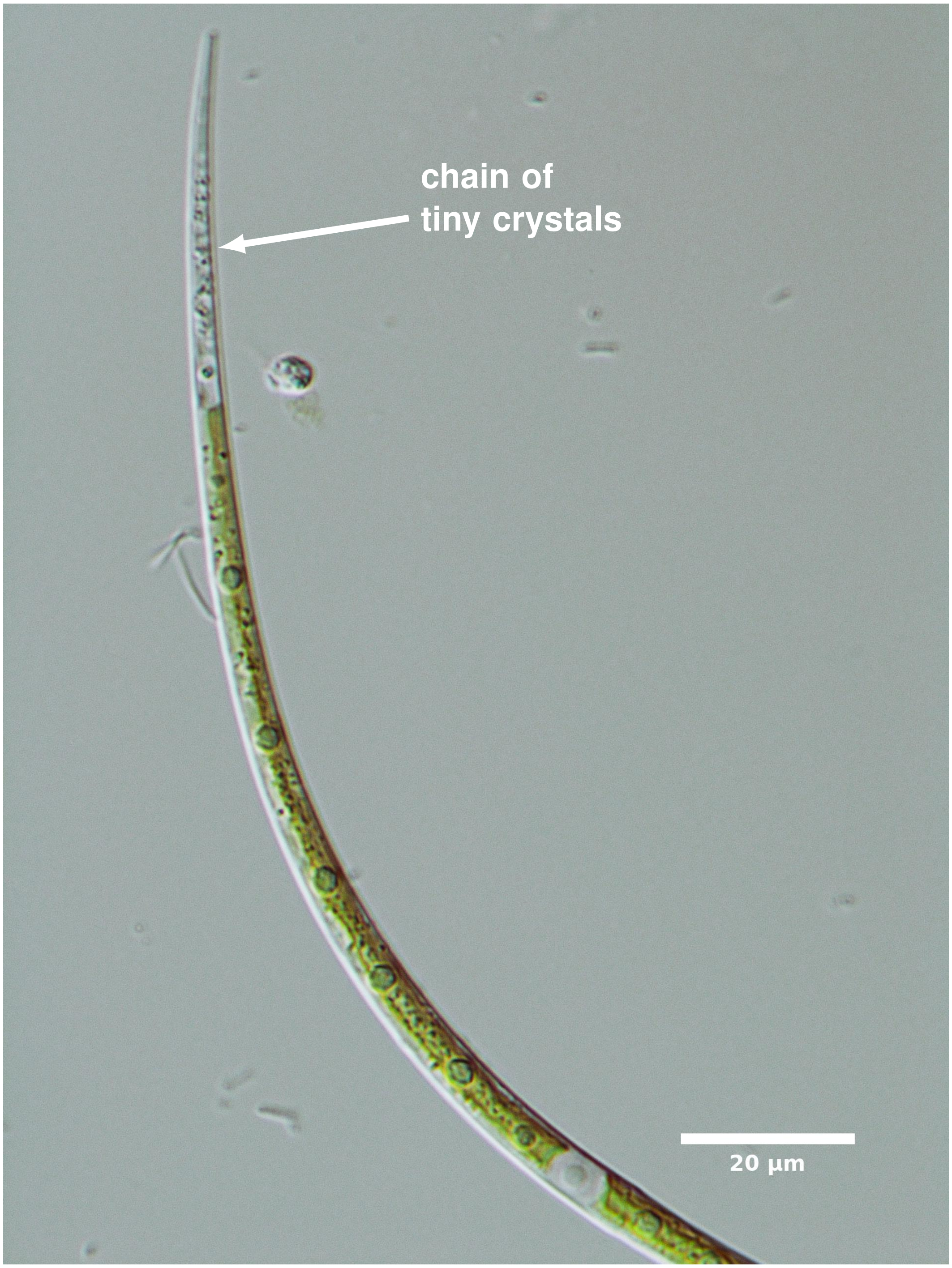


Figure 3.24: *Closterium acutum* var. *variable* (DIC), Heart Lake, Skagit County.

Figure 3.25: *Closterium acutum* var. A (DIC/DIC), Kwan Lake, Whatcom County (upper image); Thunderbird Lake, Whatcom County (lower image). Despite variation in curvature, these cells may be the same variety.

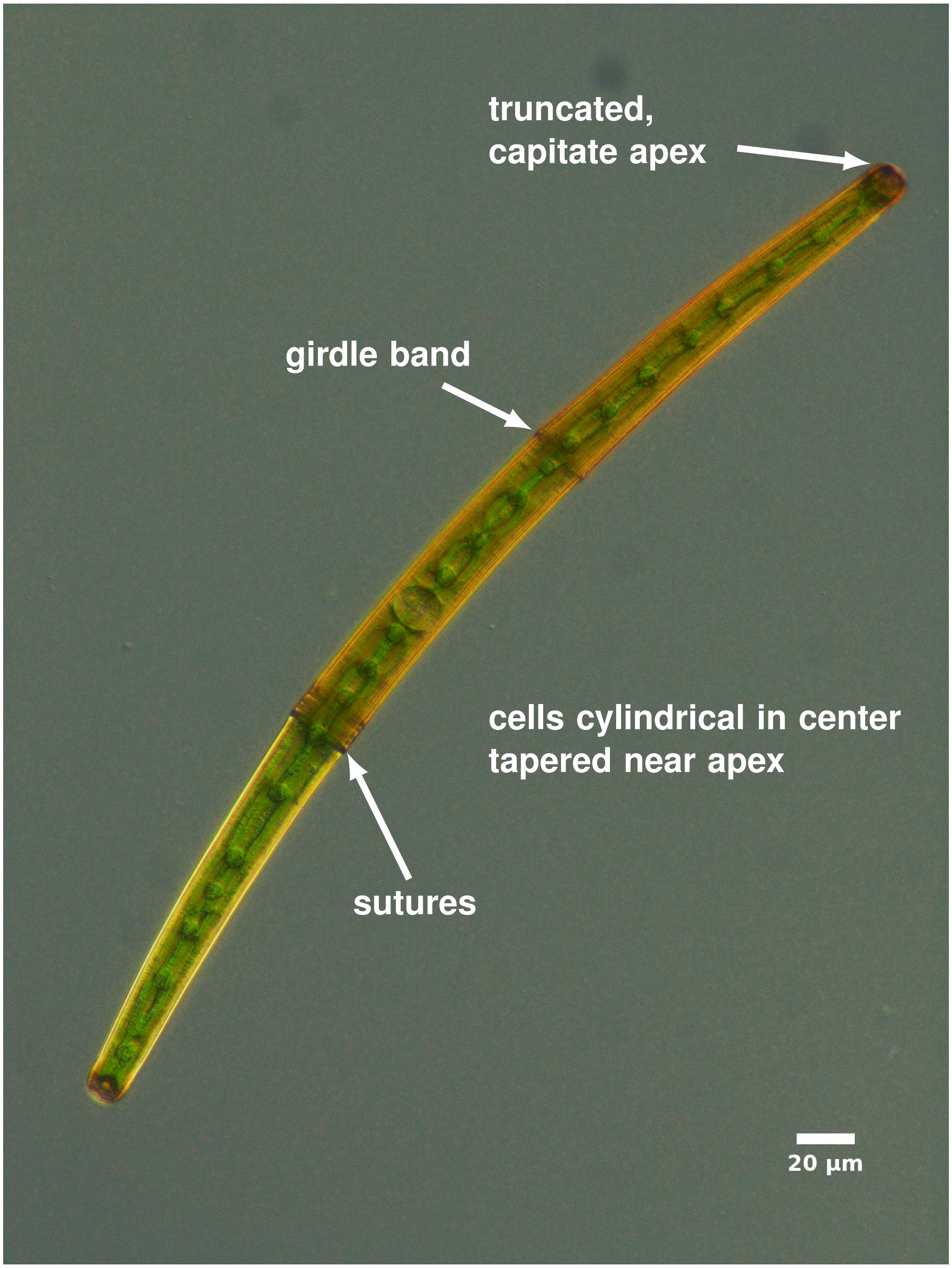


Figure 3.26: *Closterium angustatum* (DIC), Highwood Lake, Mt. Baker area, Whatcom County.

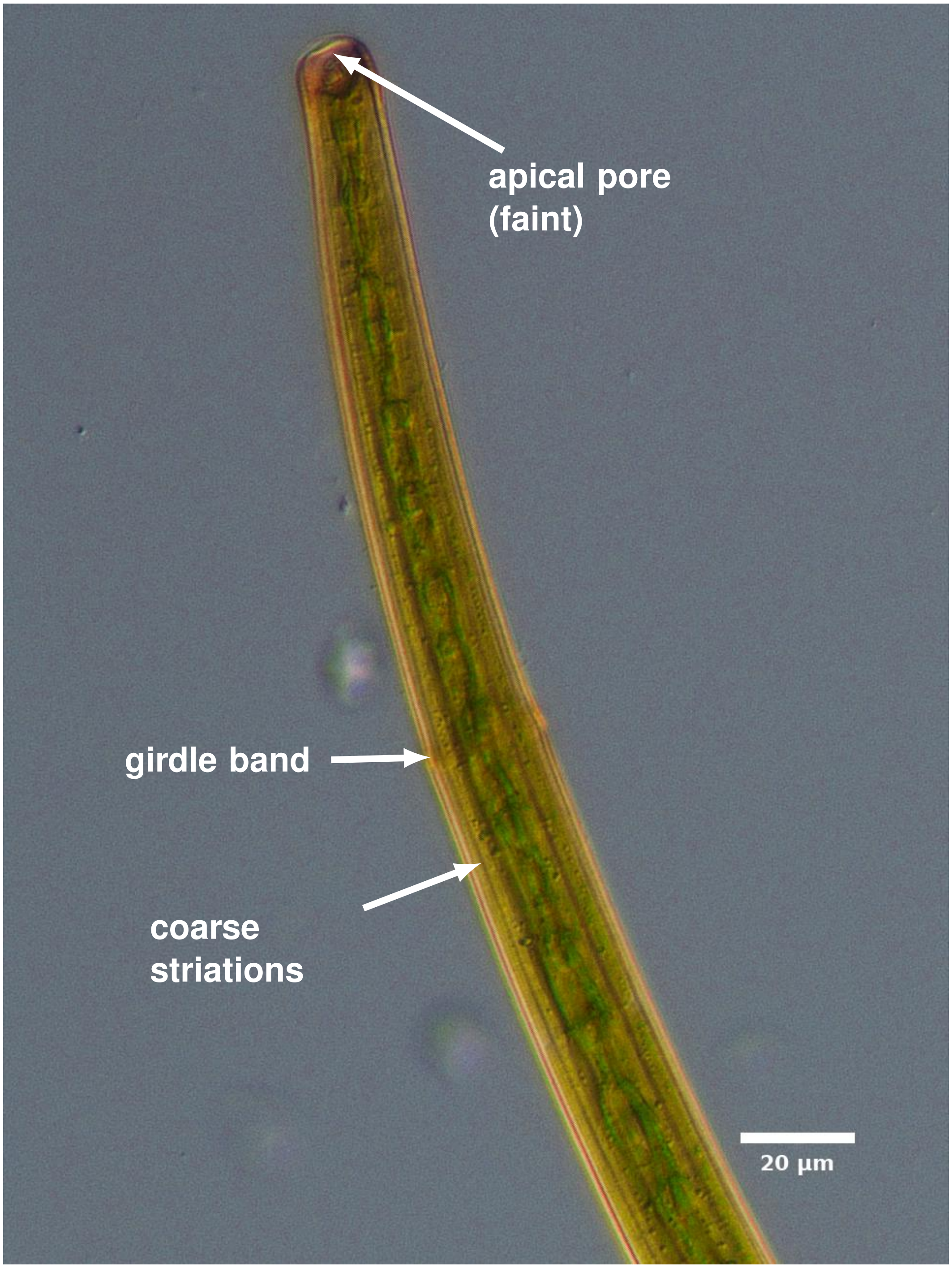


Figure 3.27: *Closterium angustatum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

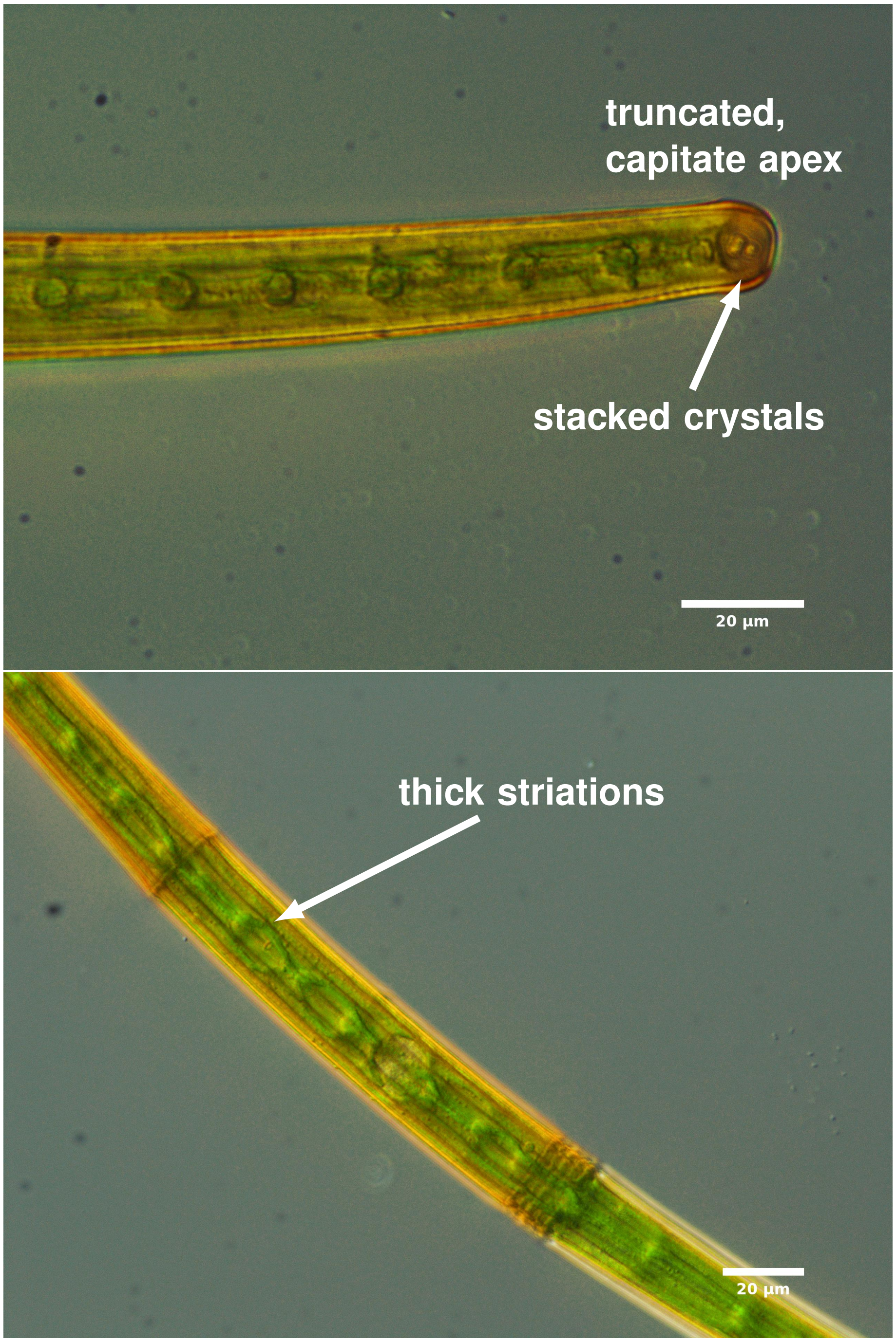


Figure 3.28: *Closterium angustatum* (DIC/DIC), Highwood Lake, Mt. Baker area, Whatcom County (upper/lower images).

Figure 3.29: *Closterium angustatum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

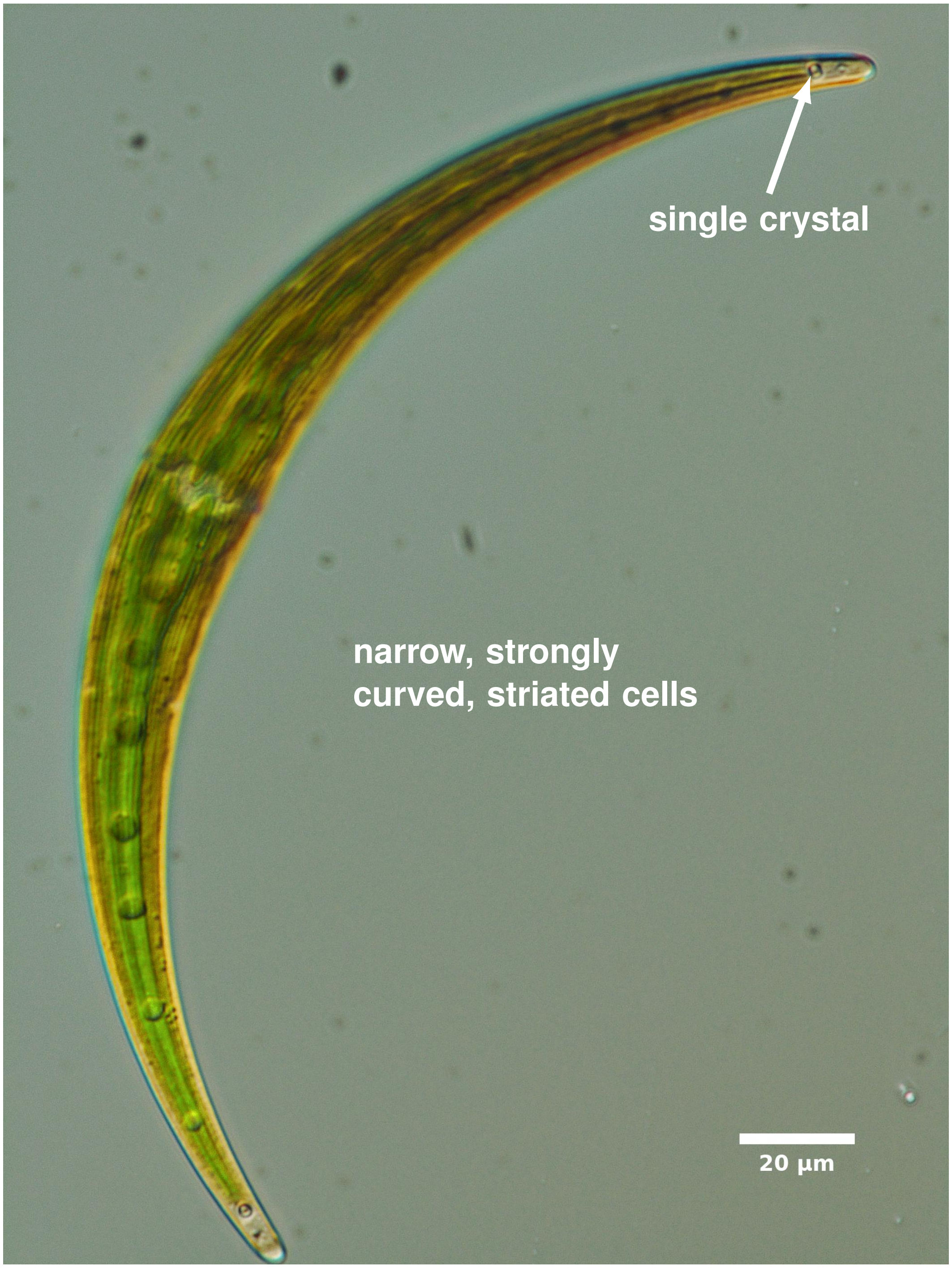


Figure 3.30: *Closterium archerianum* (DIC), Storm Lake, Snohomish County.

Figure 3.31: *Closterium archerianum* (DIC), Storm Lake, Snohomish County.

Figure 3.32: *Closterium baillyanum* (DIC), Mirror Lake, Whatcom County.

Figure 3.33: *Closterium baillyanum* (DIC), Lower Ashland Lake, Mountain Loop Highway, Snohomish County.

Figure 3.34: *Closterium baillyanum* (DIC), Summer Lake, Skagit County.

Figure 3.35: *Closterium baillyanum* (DIC), Mirror Lake, Whatcom County.

Figure 3.36: *Closterium baillyanum* var. *alpinum* (DIC), small floating bog along Morris Valley Road near Harrison, BC.

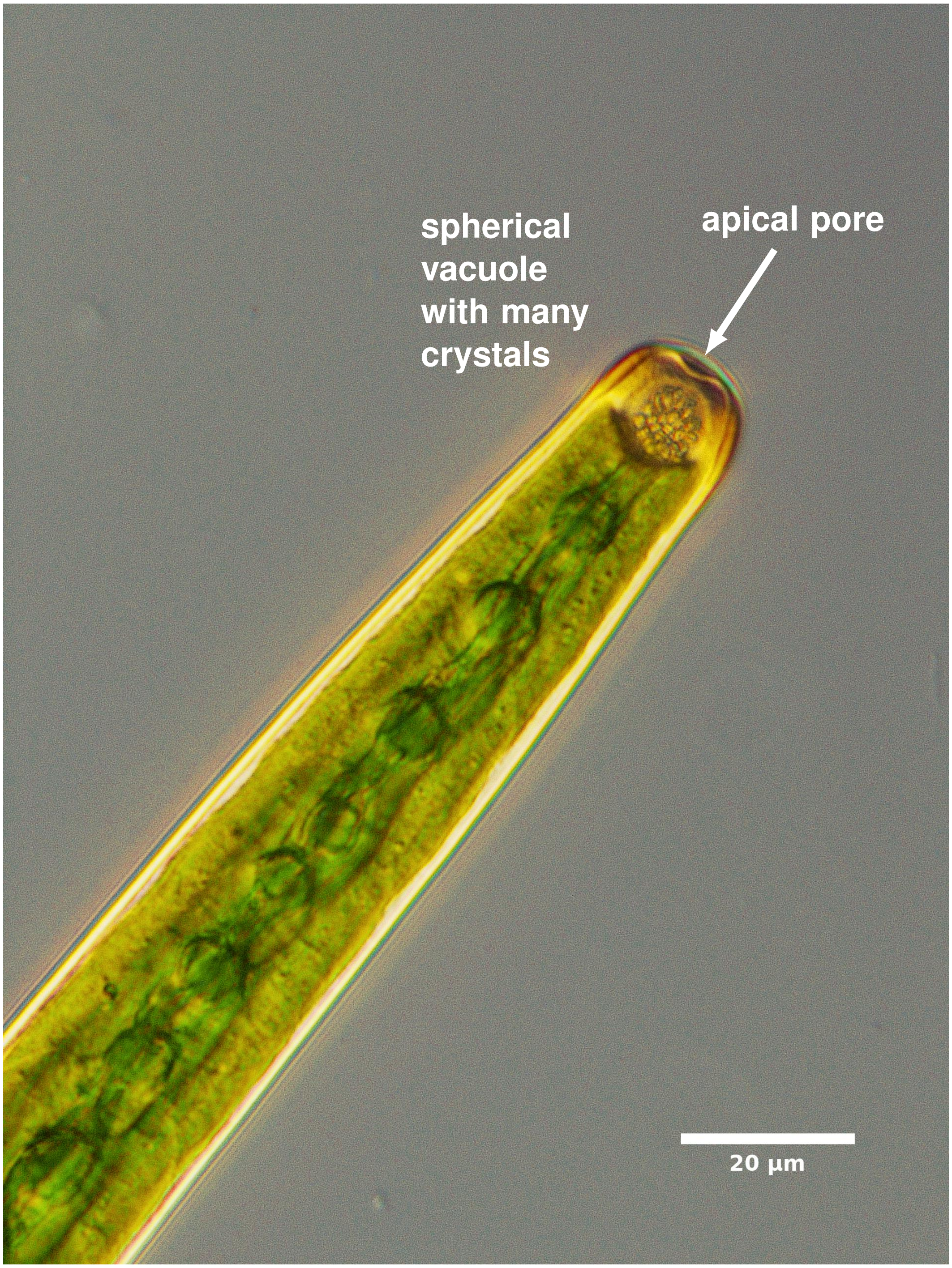


Figure 3.37: *Closterium baillyanum* var. *alpinum* (DIC), small floating bog along Morris Valley Road near Harrison, BC.

Figure 3.38: *Closterium braunii* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.39: *Closterium braunii* (DIC), Summer Lake, Skagit County.

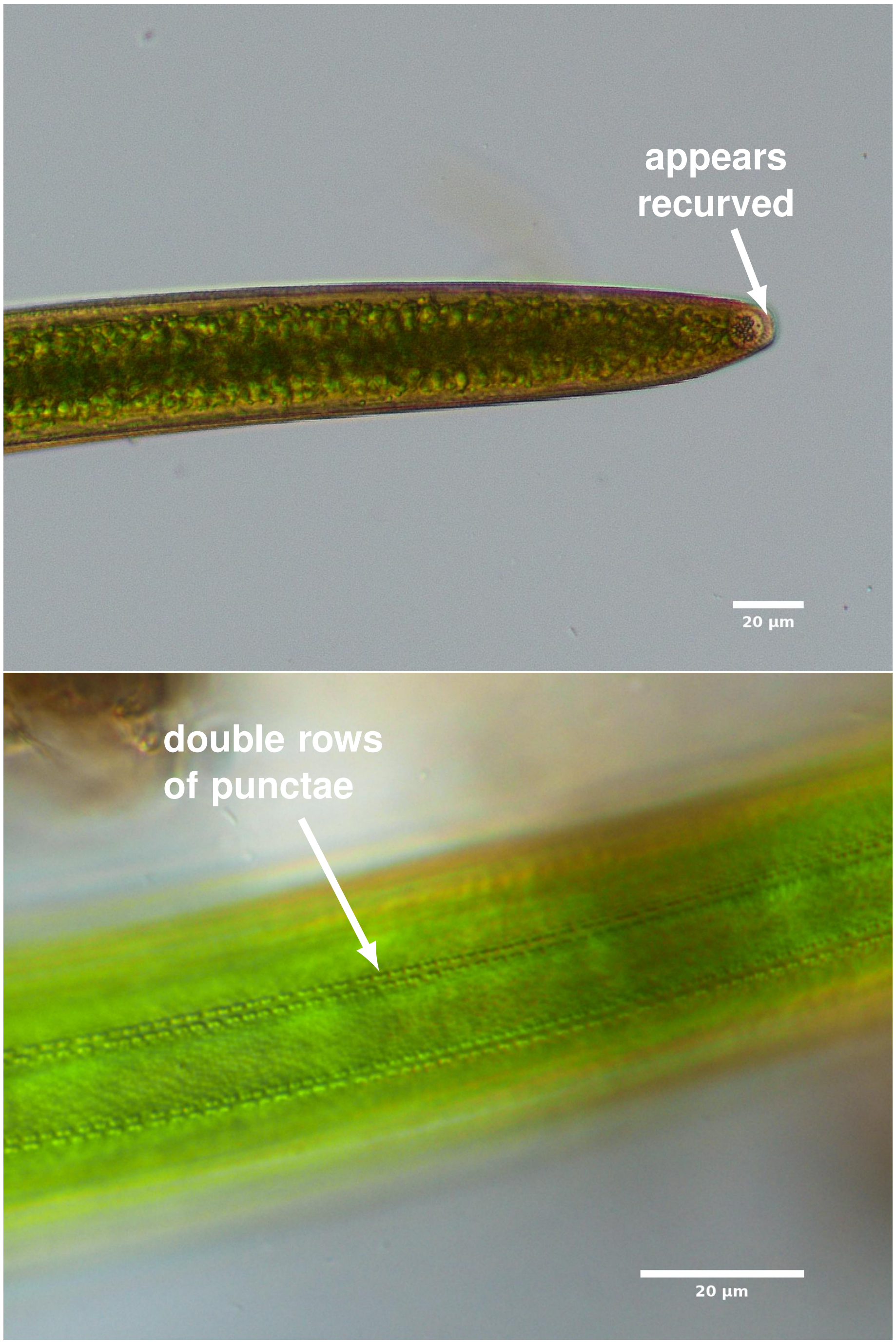


Figure 3.40: *Closterium braunii* (DIC/DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County (upper/lower images).

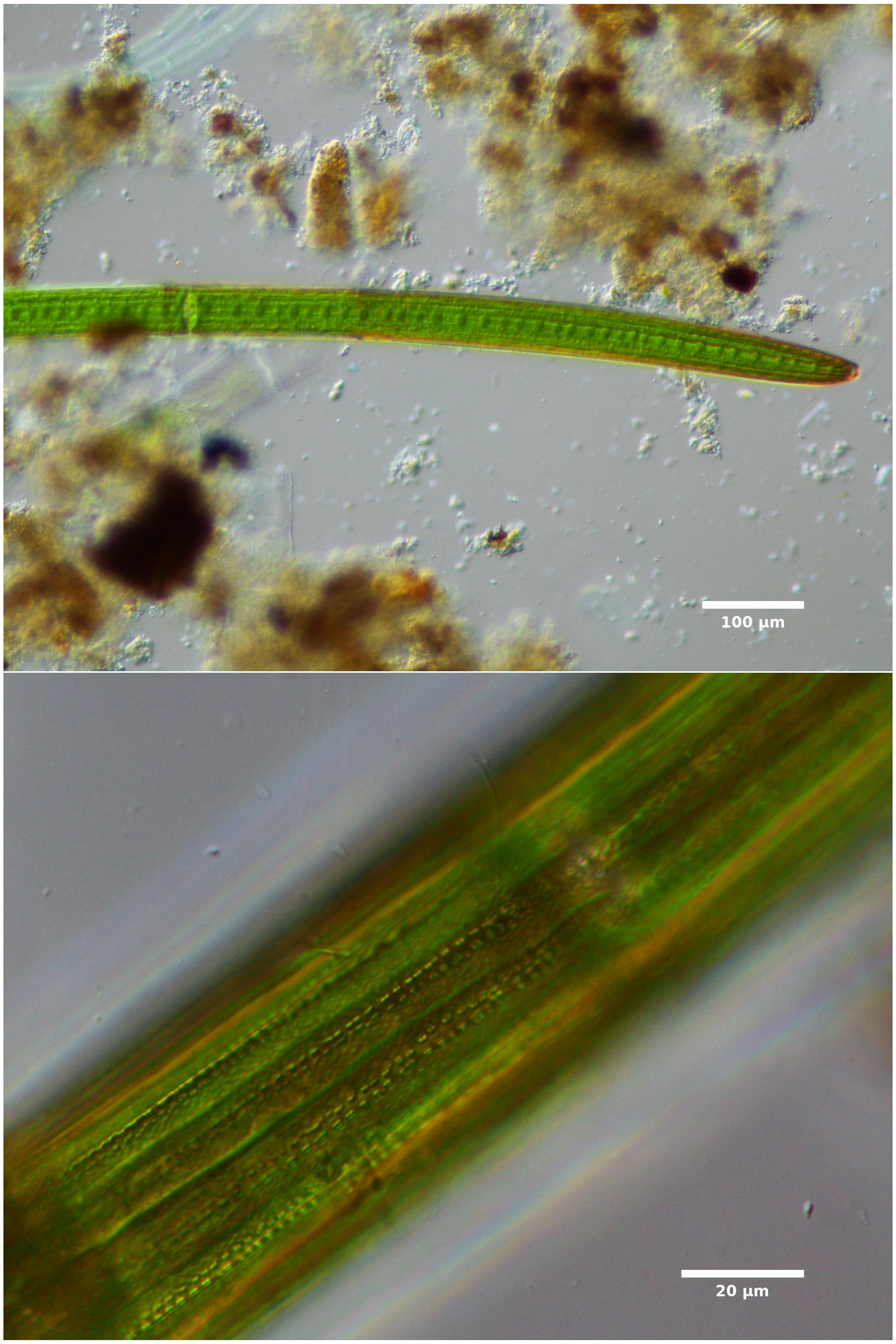


Figure 3.41: *Closterium braunii* (DIC/DIC), Beaver Pond Lake, Whatcom County (upper/lower images).

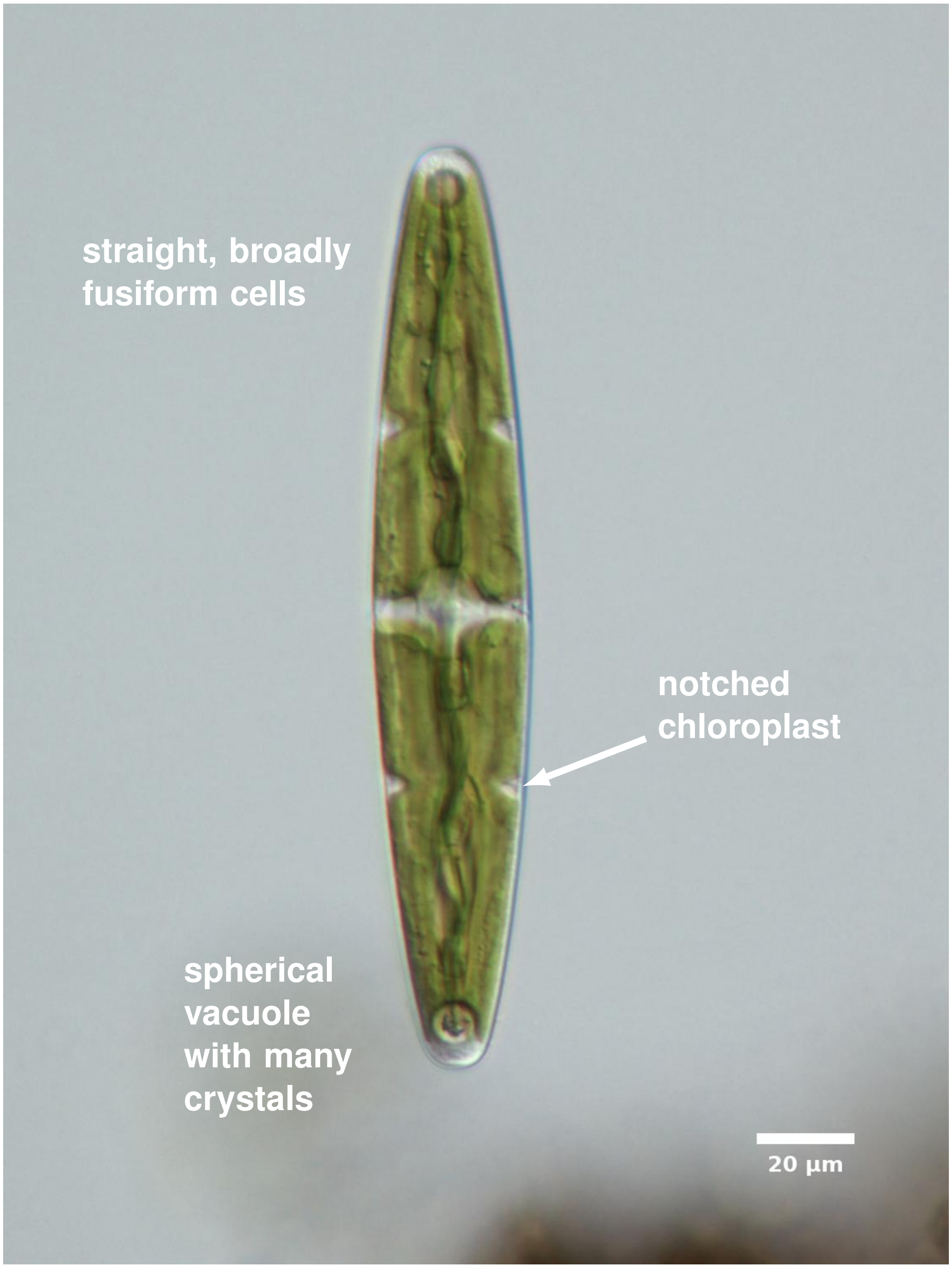


Figure 3.42: *Closterium closterioides* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.43: *Closterium closterioides* (DIC), Lower Ashland Lake, Mountain Loop Highway, Snohomish County.

Figure 3.44: *Closterium closterioides* (DIC), Pine Lake, Whatcom County.

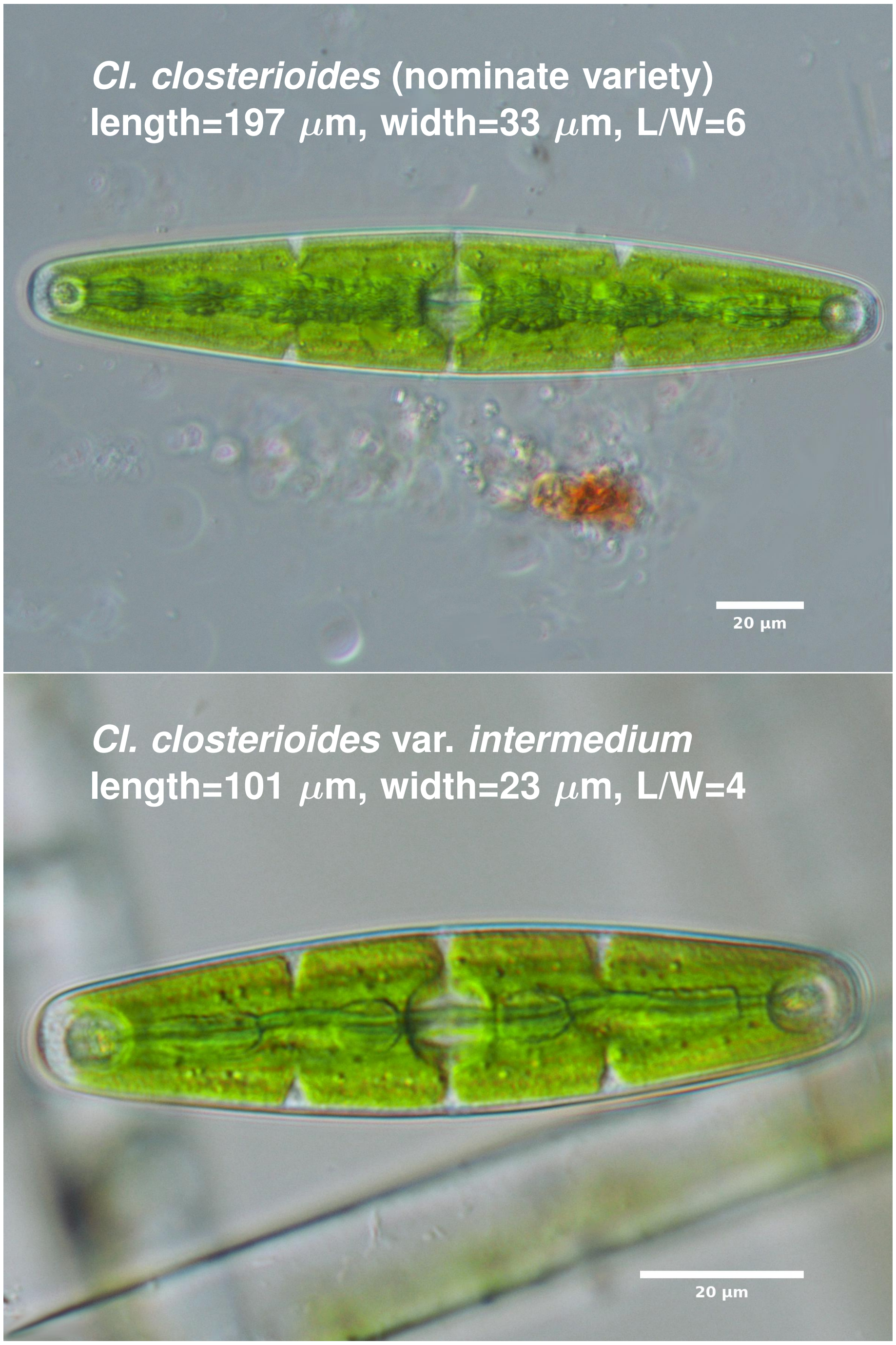


Figure 3.45: *Closterium closterioides* and *Closterium closterioides* var. *intermedium* (DIC/DIC), samples collected on same date, Lower Ashland Lake, Mountain Loop Highway, Snohomish County (upper/lower images).

Figure 3.46: *Closterium closterioides* var. *intermedium* (DIC), Upper Anderson Lake, Mt. Baker area, Whatcom County.

Figure 3.47: *Closterium closterioides* var. *intermedium* (DIC), Chain Lake, Gifford Pinchot National Forest, Skamania County.

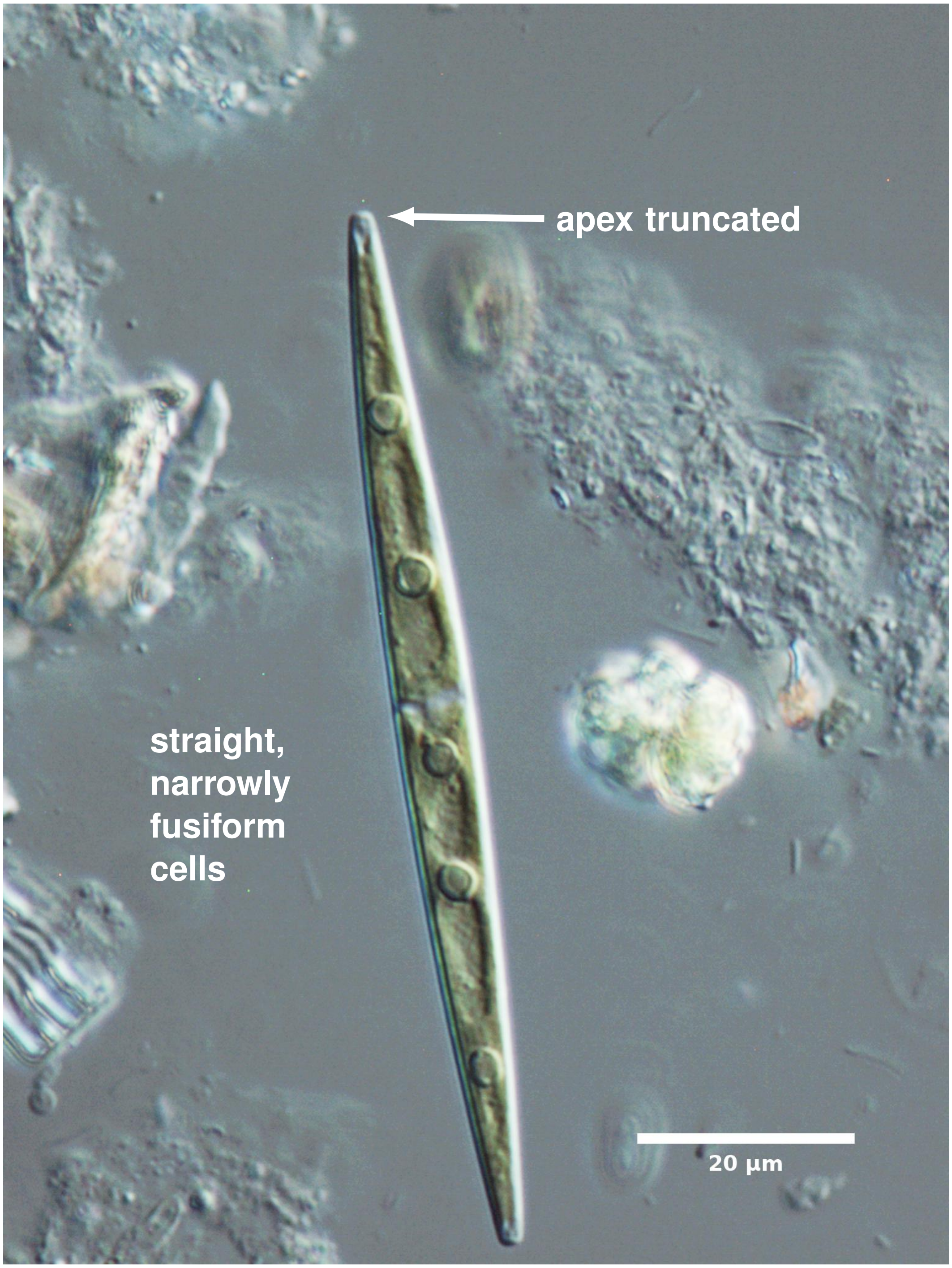


Figure 3.48: *Closterium* cf. *cornu* (DIC), Bear Lake, Mountain Loop Highway, Snohomish County.

Figure 3.49: *Closterium* cf. *cornu* (DIC), Heather Lake, Mountain Loop Highway, Snohomish County.

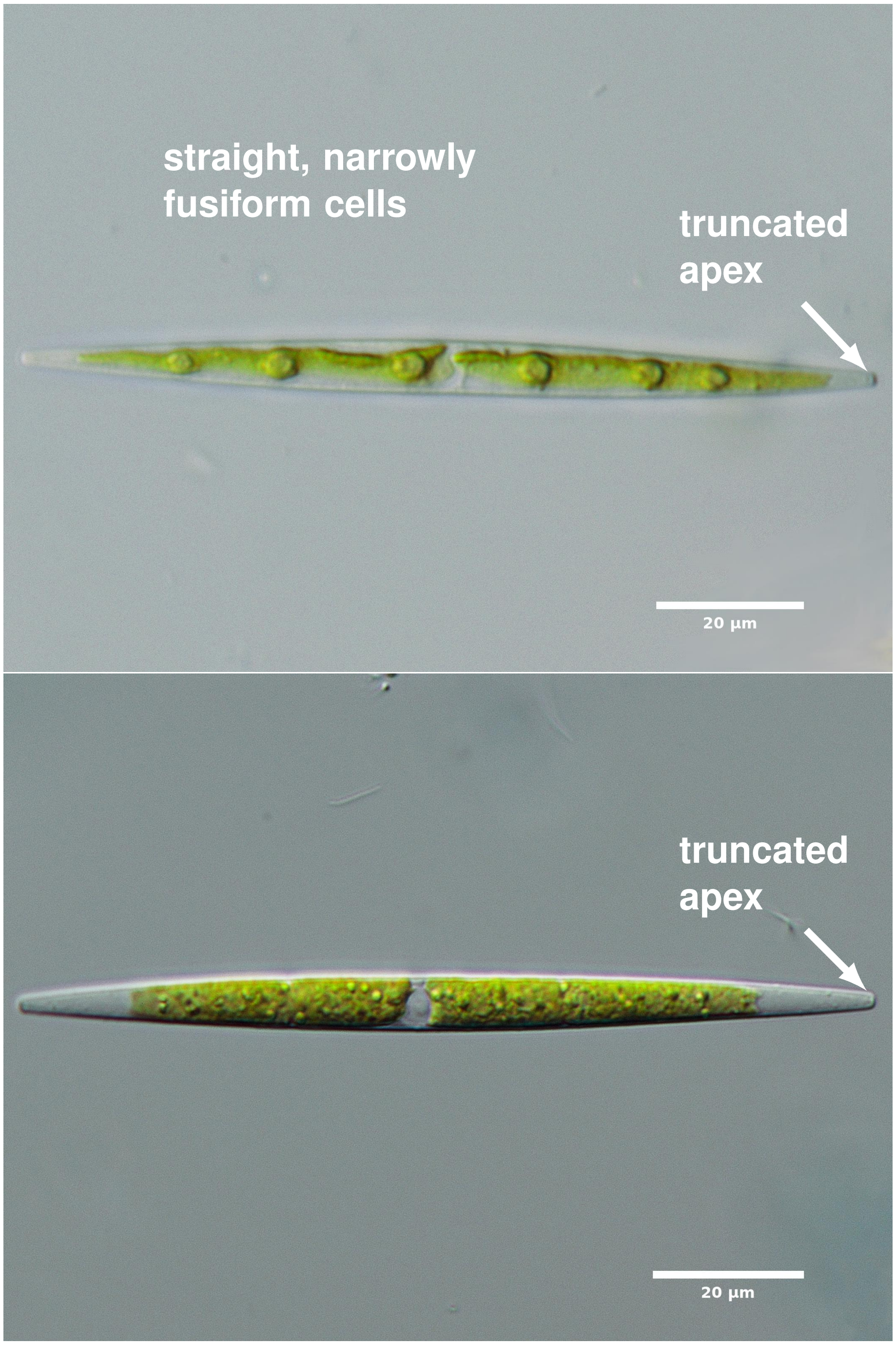


Figure 3.50: *Closterium* cf. *cornu* (DIC/DIC), Bear Lake, Mountain Loop Highway, Snohomish County (upper/lower images). Cell in lower image has damaged chloroplasts - chloroplast should extend nearly to apex.

Figure 3.51: *Closterium costatum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.52: *Closterium costatum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.53: *Closterium costatum* (DIC), Bear Lake, Mountain Loop Highway, Snohomish County.

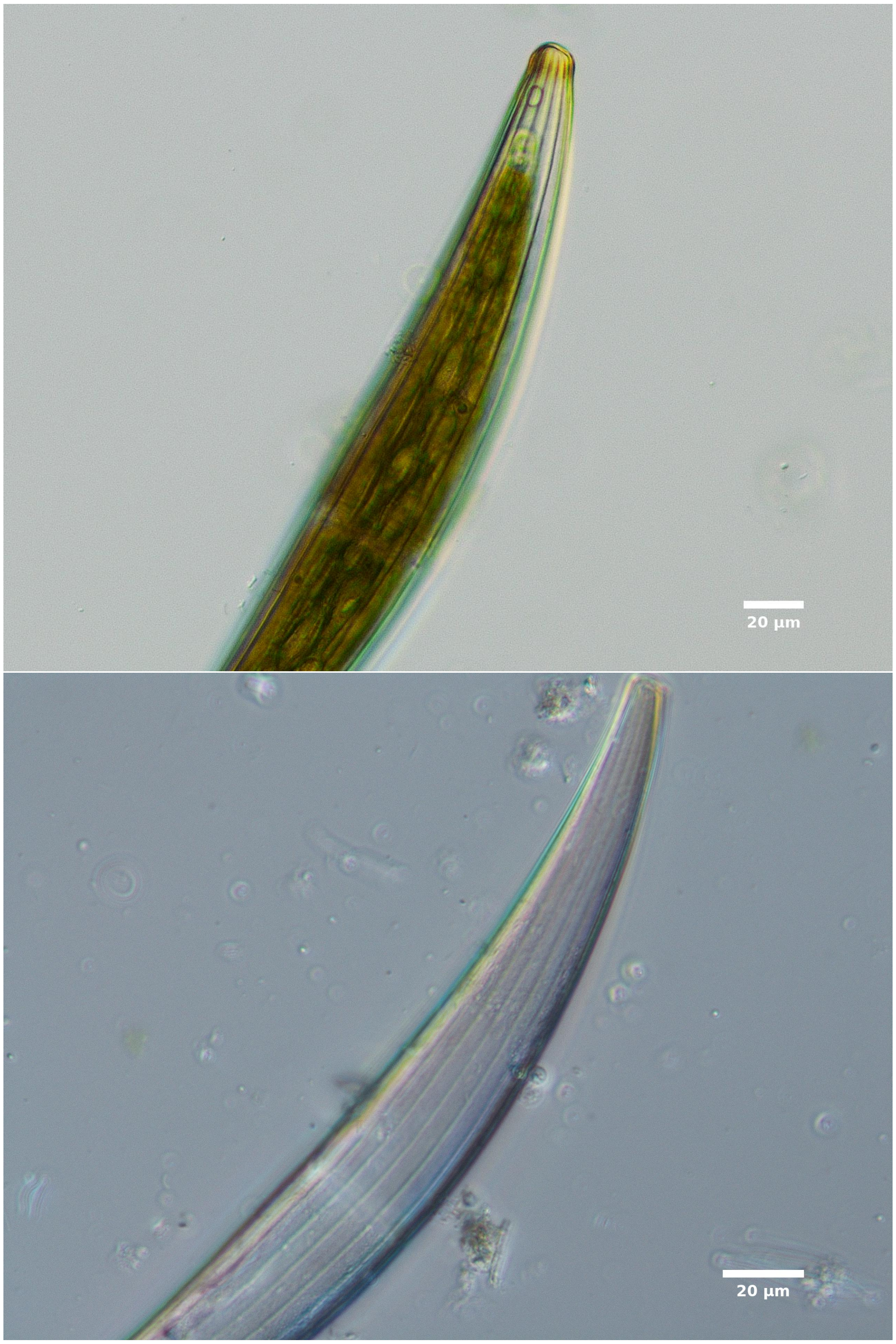


Figure 3.54: *Closterium costatum* wall striations (DIC/DIC), Lake Evan, Mountain Loop Highway, Snohomish County (upper/lower images).

Figure 3.55: *Closterium costatum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

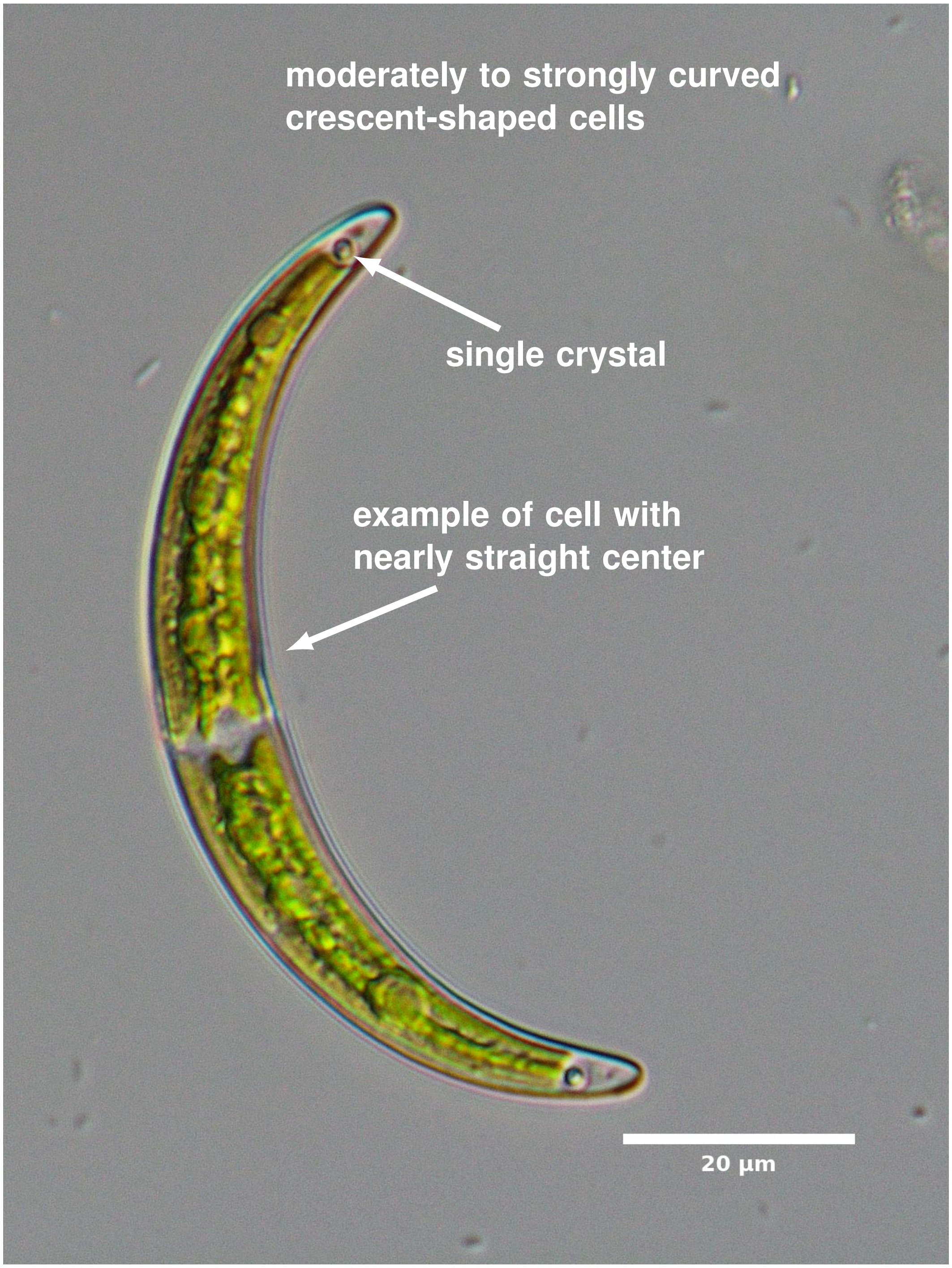


Figure 3.56: *Closterium cynthia* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.57: *Closterium cynthia* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

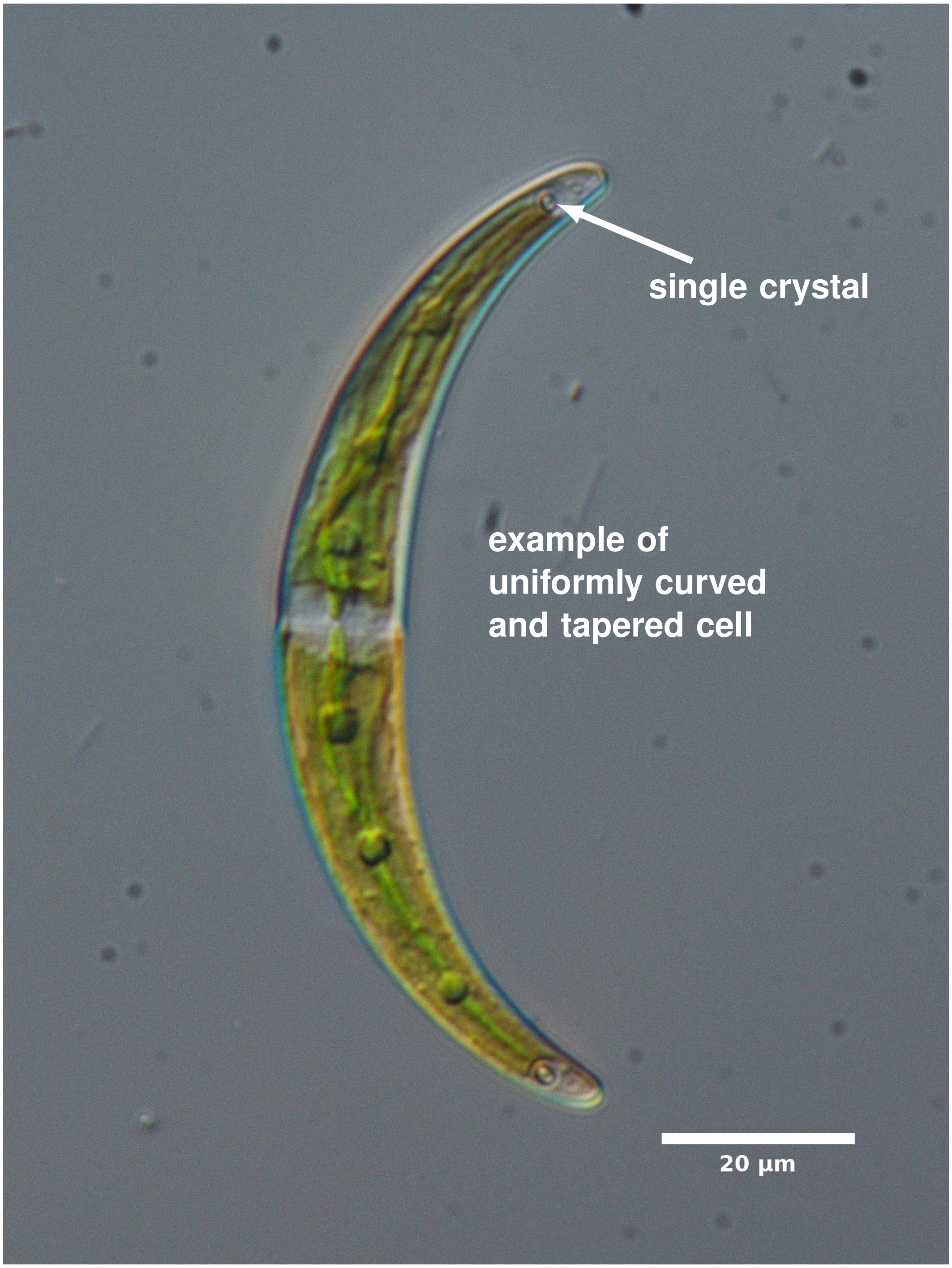


Figure 3.58: *Closterium cynthia* (DIC), Picture Lake, Mt. Baker area, Whatcom County.

Figure 3.59: *Closterium cynthia* (DIC), Lake Twenty-two, Mountain Loop Highway, Snohomish County.

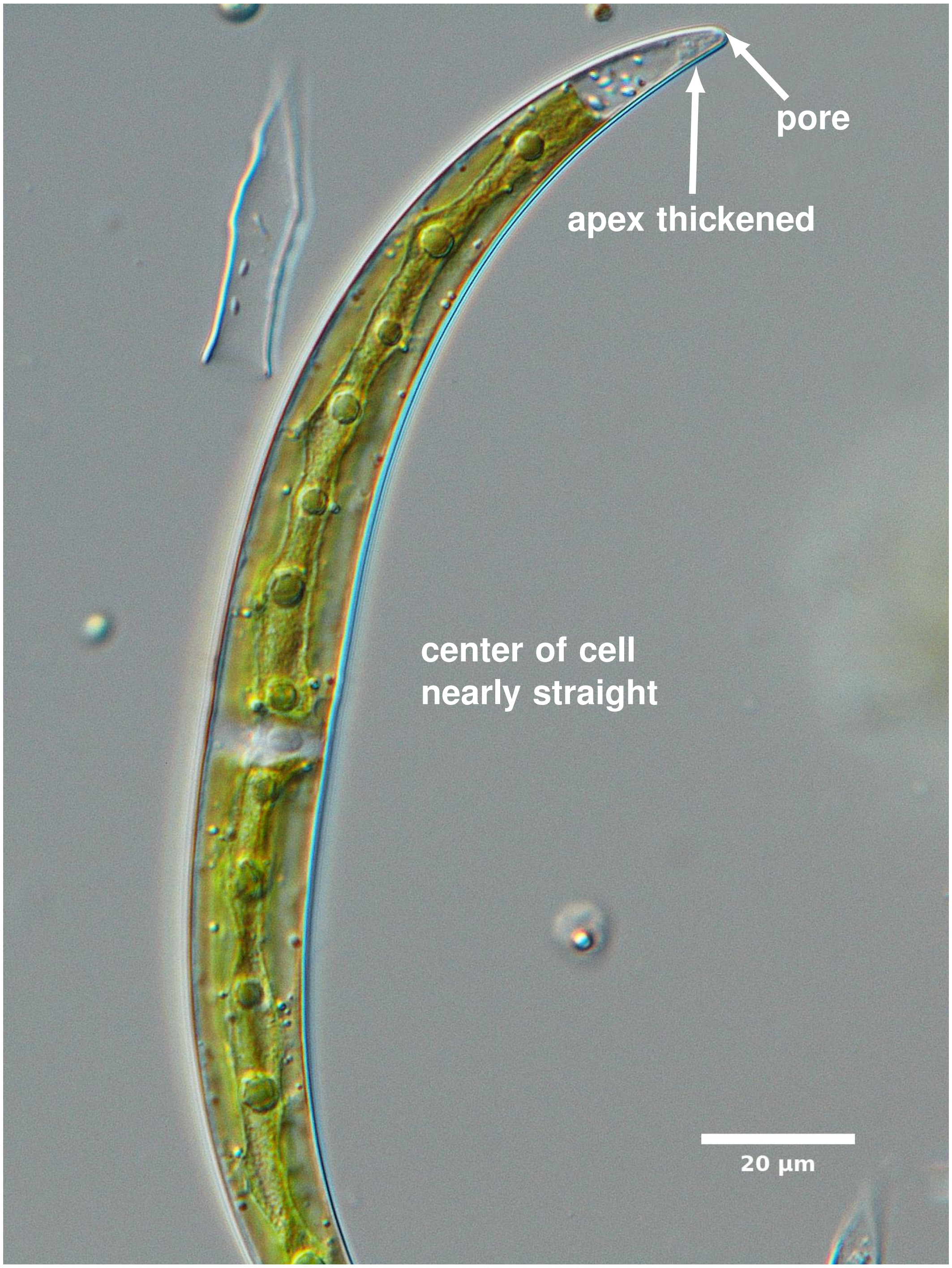


Figure 3.60: *Closterium dianae* (DIC), Big Twin Lake (eastern Washington), Okanogan County.

Figure 3.61: *Closterium dianae* (DIC), Big Twin Lake (eastern Washington), Okanogan County.

Figure 3.62: *Closterium dianae* (DIC), Lake Everett, Skagit County.

Figure 3.63: *Closterium dianae* cf. var. *minus* (DIC), small pond on trail to Big Four Ice Caves, Mountain Loop Highway, Snohomish County.

Figure 3.64: *Closterium dianae* cf. var. *minus* (DIC), Bear Lake, Mountain Loop Highway, Snohomish County.

Figure 3.65: *Closterium* cf. *dianae* (DIC), Squalicum Lake, Whatcom County.

Figure 3.66: *Closterium* cf. *dianae* (DIC), Beaver Pond Lake, Whatcom County.

Figure 3.67: *Closterium didymotocum* (DIC), small floating bog along Morris Valley Road near Harrison, BC.

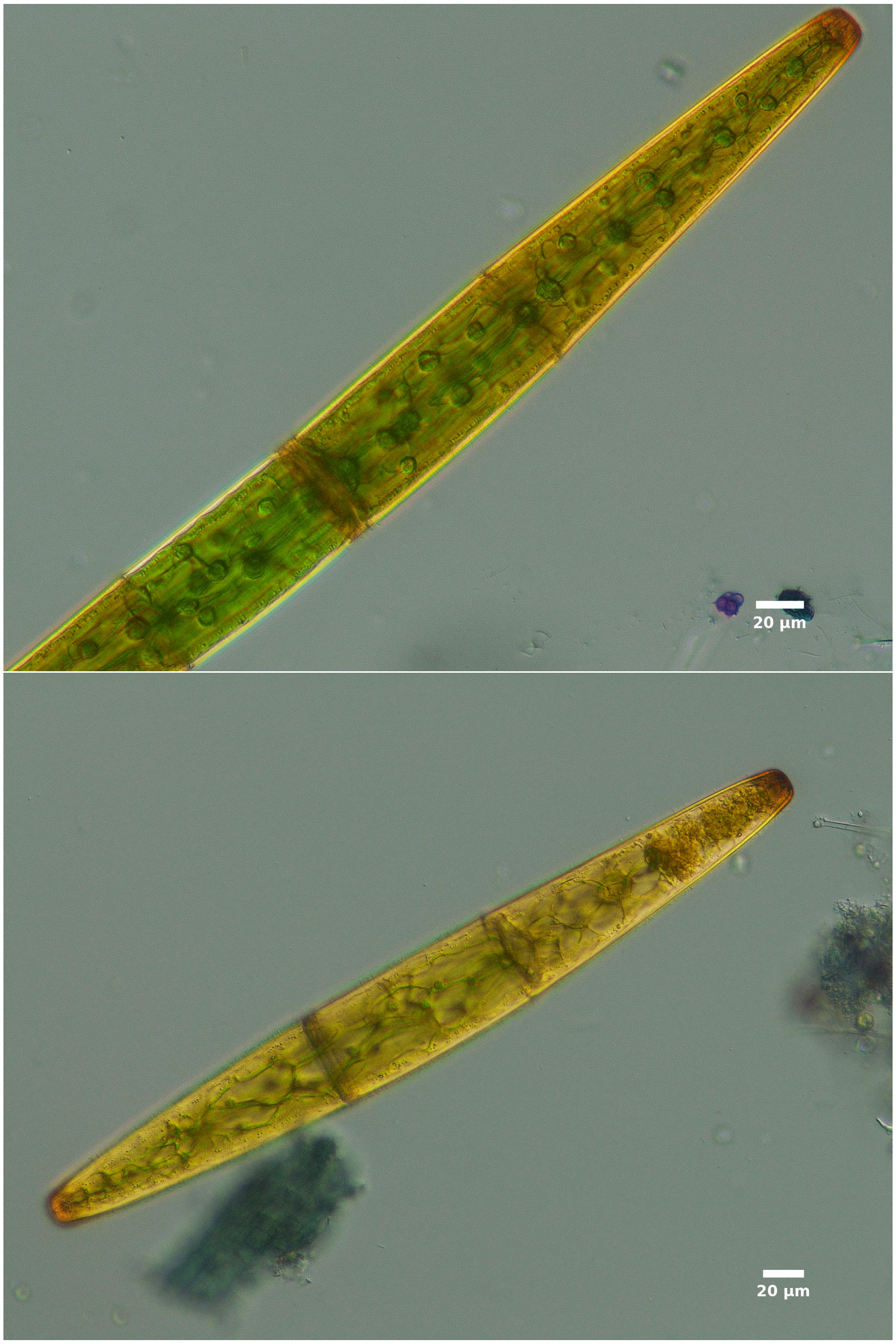


Figure 3.68: *Closterium didymotocum* girdle bands (DIC/DIC), small floating bog along Morris Valley Road near Harrison, BC (upper/lower images).

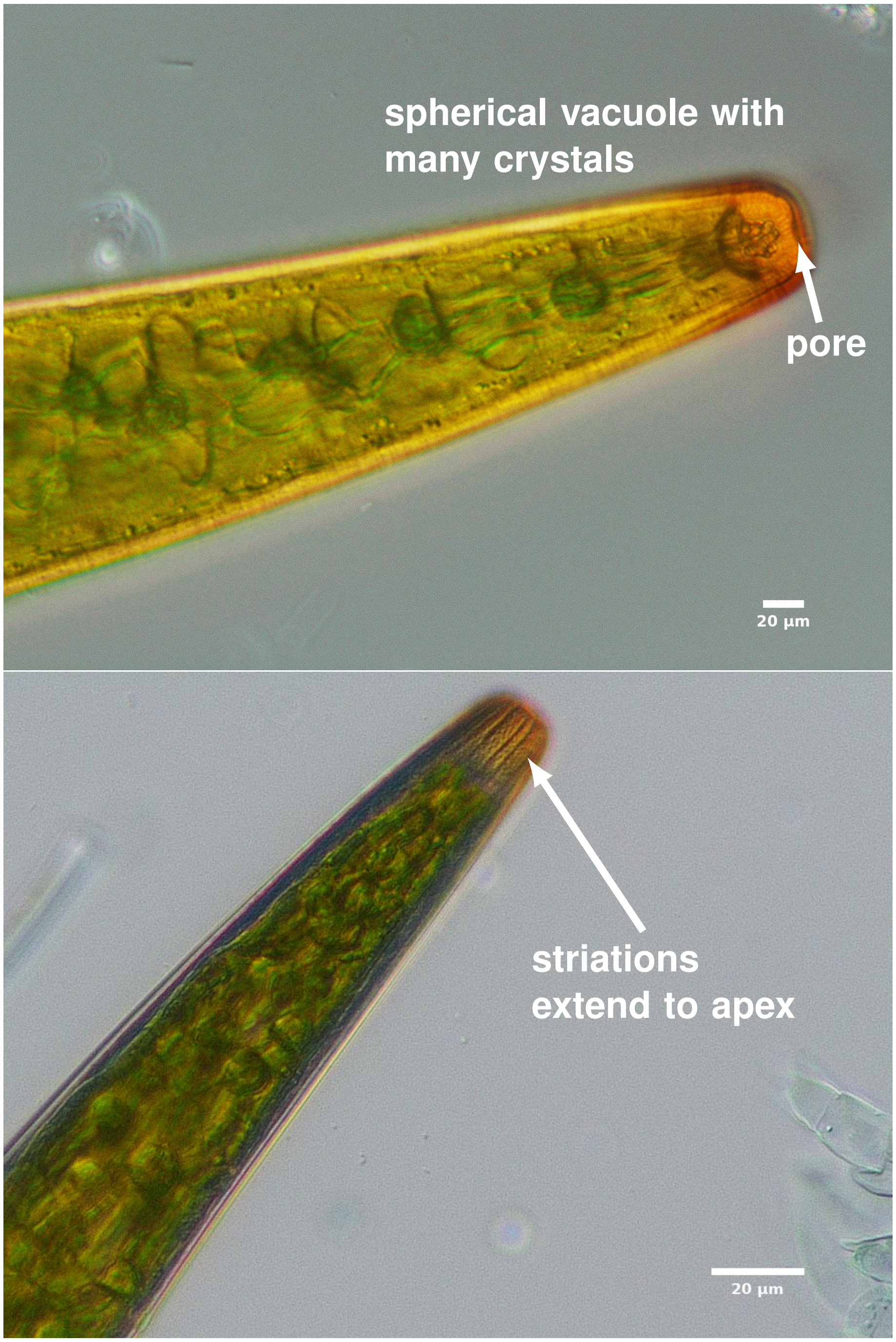


Figure 3.69: *Closterium didymotocum* (DIC/DIC), small floating bog along Morris Valley Road near Harrison, BC quality sampling site, Snohomish County (upper/lower images).

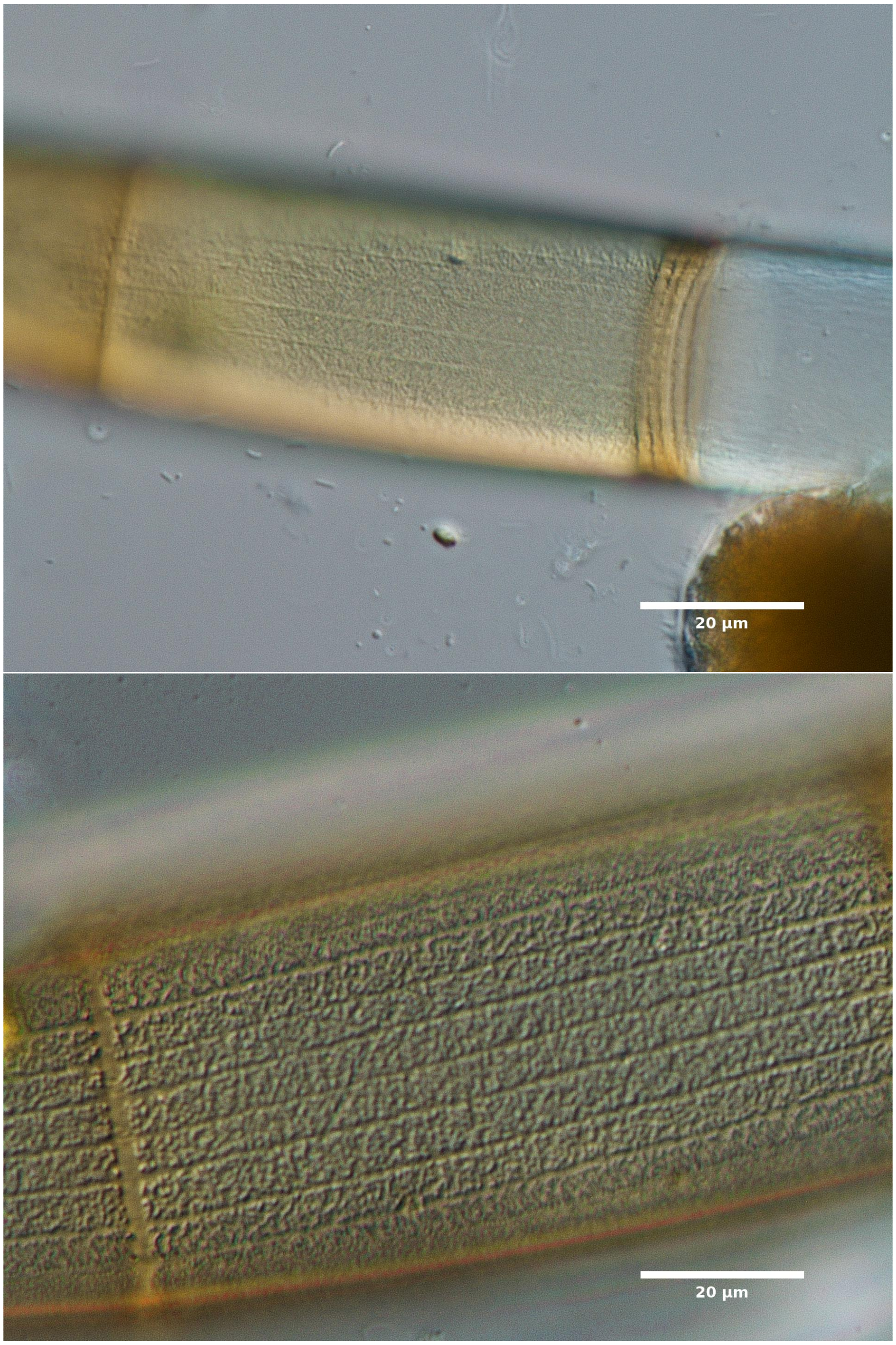


Figure 3.70: *Closterium didymotocum* wall striations and punctae (DIC/DIC), small floating bog along Morris Valley Road near Harrison, BC (upper/lower images).

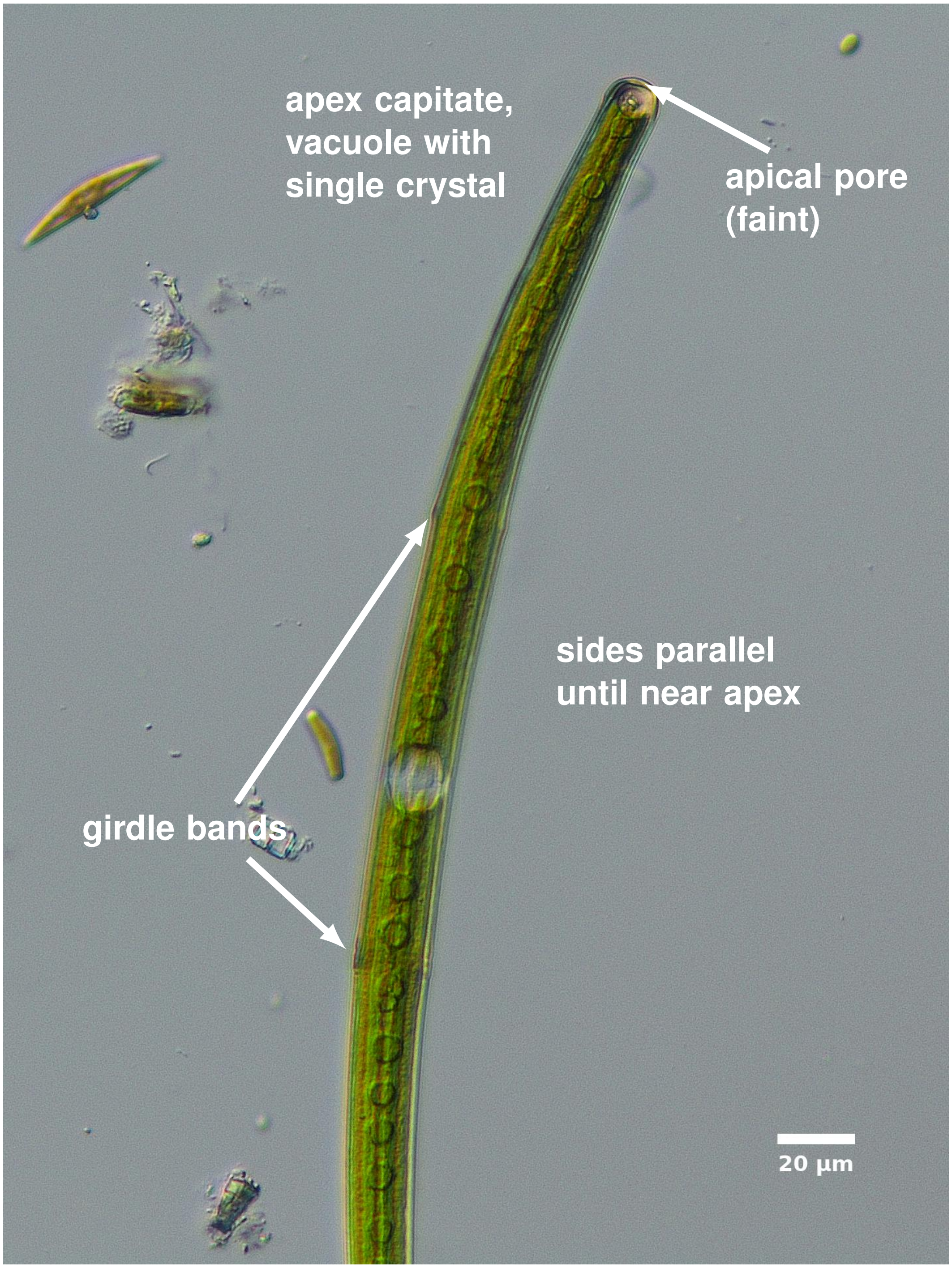


Figure 3.71: *Closterium directum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

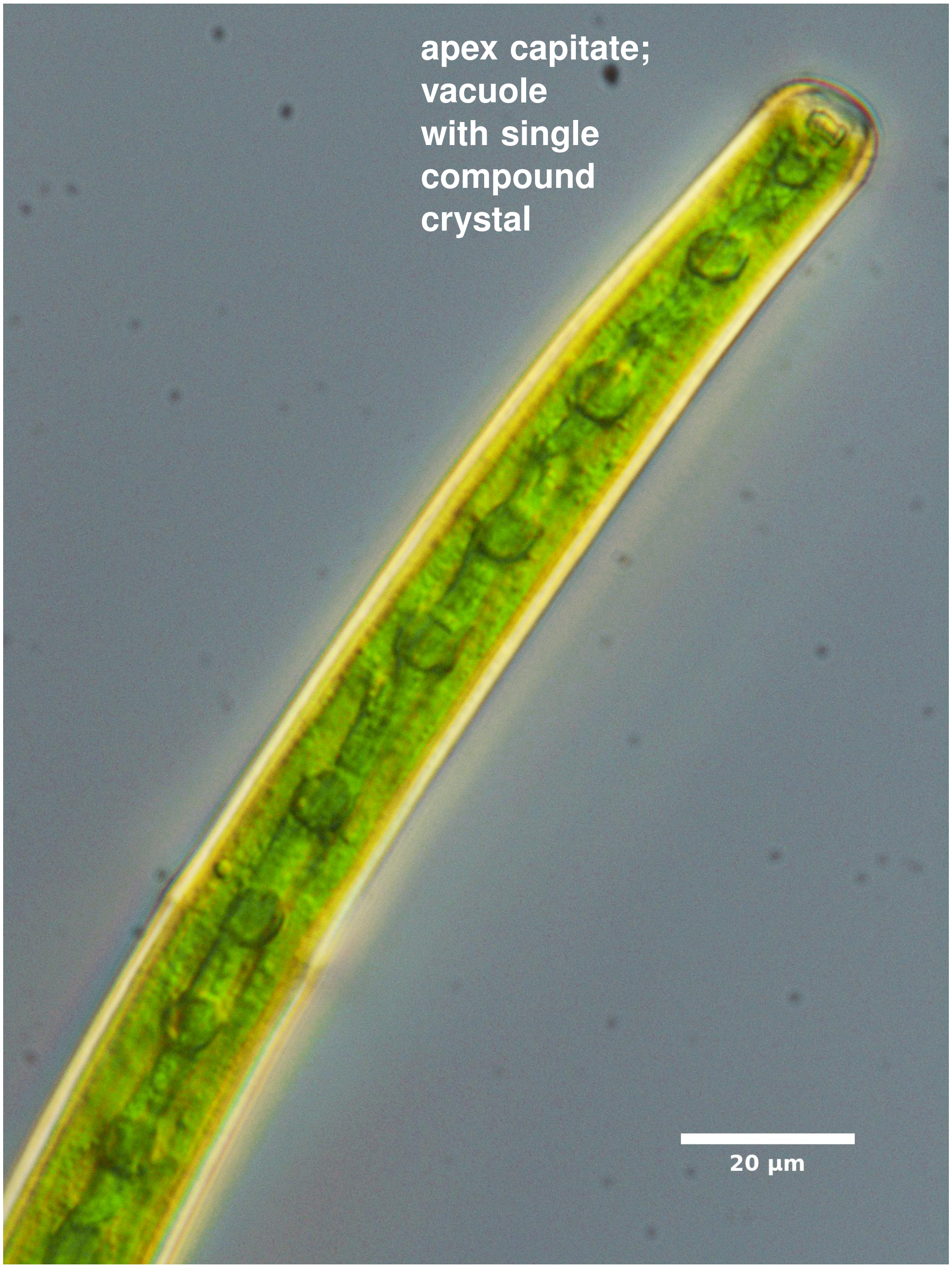


Figure 3.72: *Closterium directum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.73: *Closterium directum* girdle bands and wall striations (DIC/DIC), Boardman Lake, Mountain Loop Highway, Snohomish County (upper/lower images).

Figure 3.74: *Closterium ehrenbergii* (DIC), small residential pond, Whatcom County.

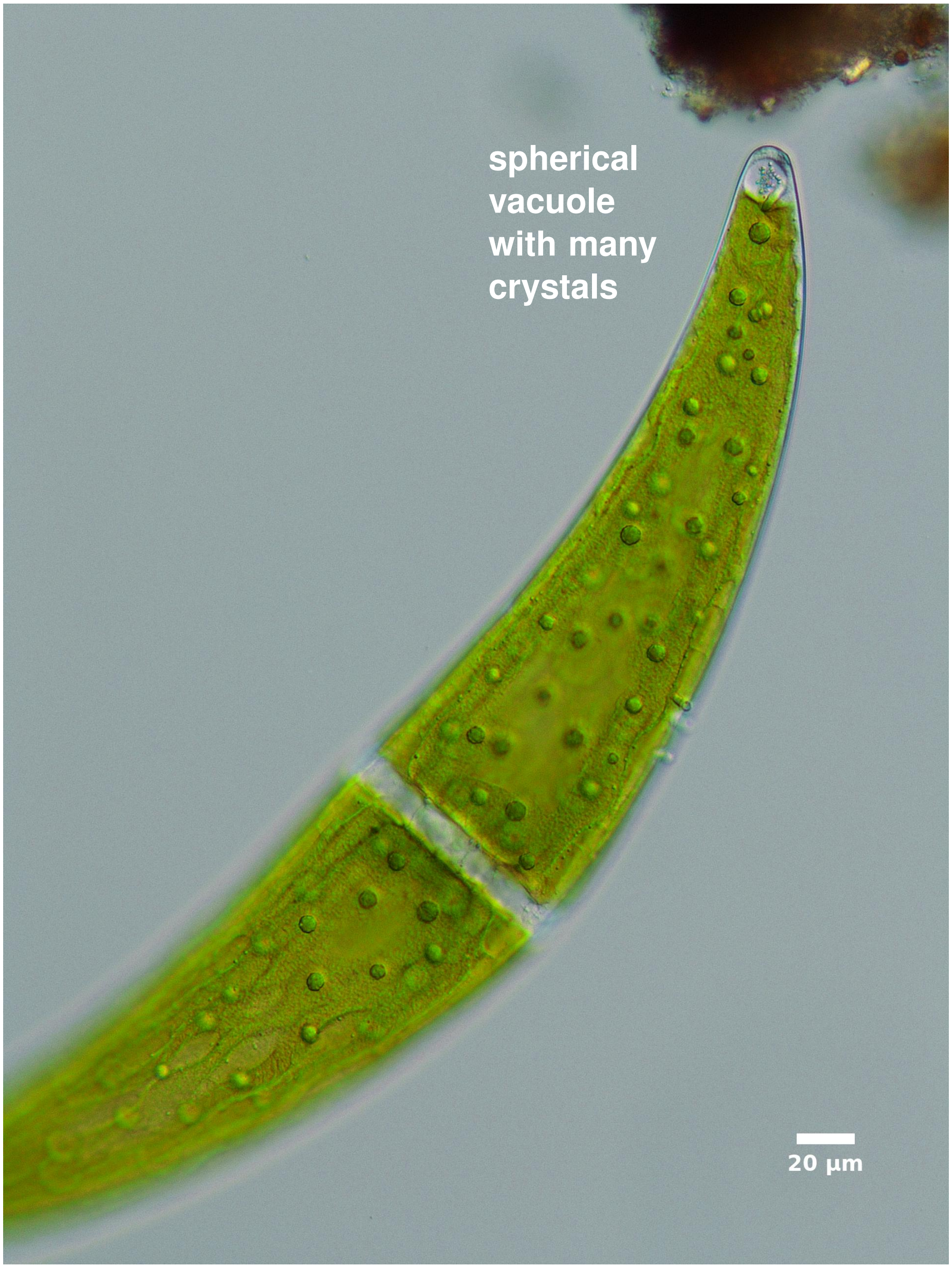


Figure 3.75: *Closterium ehrenbergii* (DIC), Cedar Hills stormwater treatment pond, Whatcom County.

Figure 3.76: *Closterium ehrenbergii* (DIC), Lake Campbell (eastern Washington), Okanogan County.

Figure 3.77: *Closterium ehrenbergii* conjugation and zygote formation (DIC), small residential pond, Whatcom County.

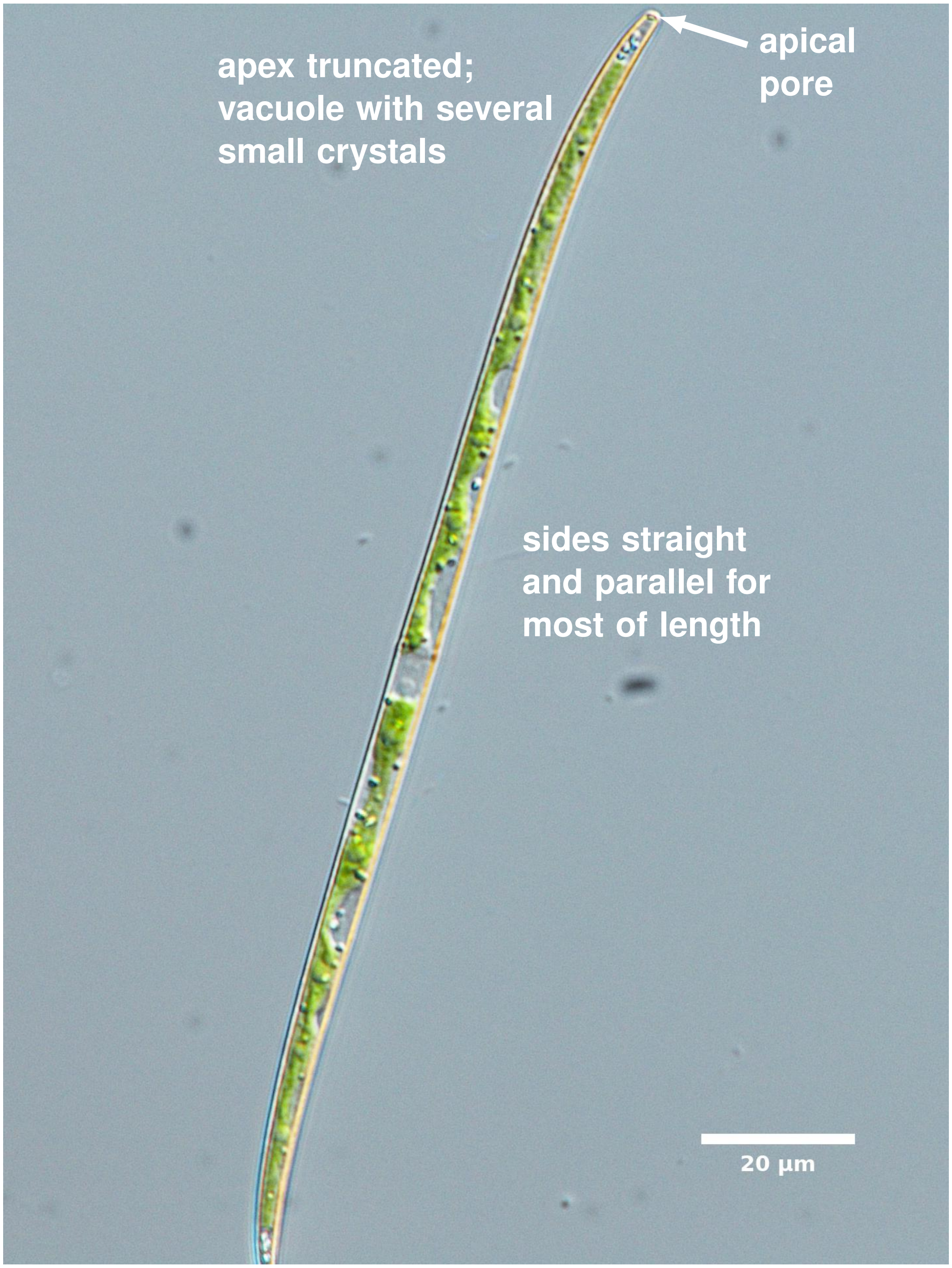


Figure 3.78: *Closterium gracile* (DIC), Lake Louise, Whatcom County.

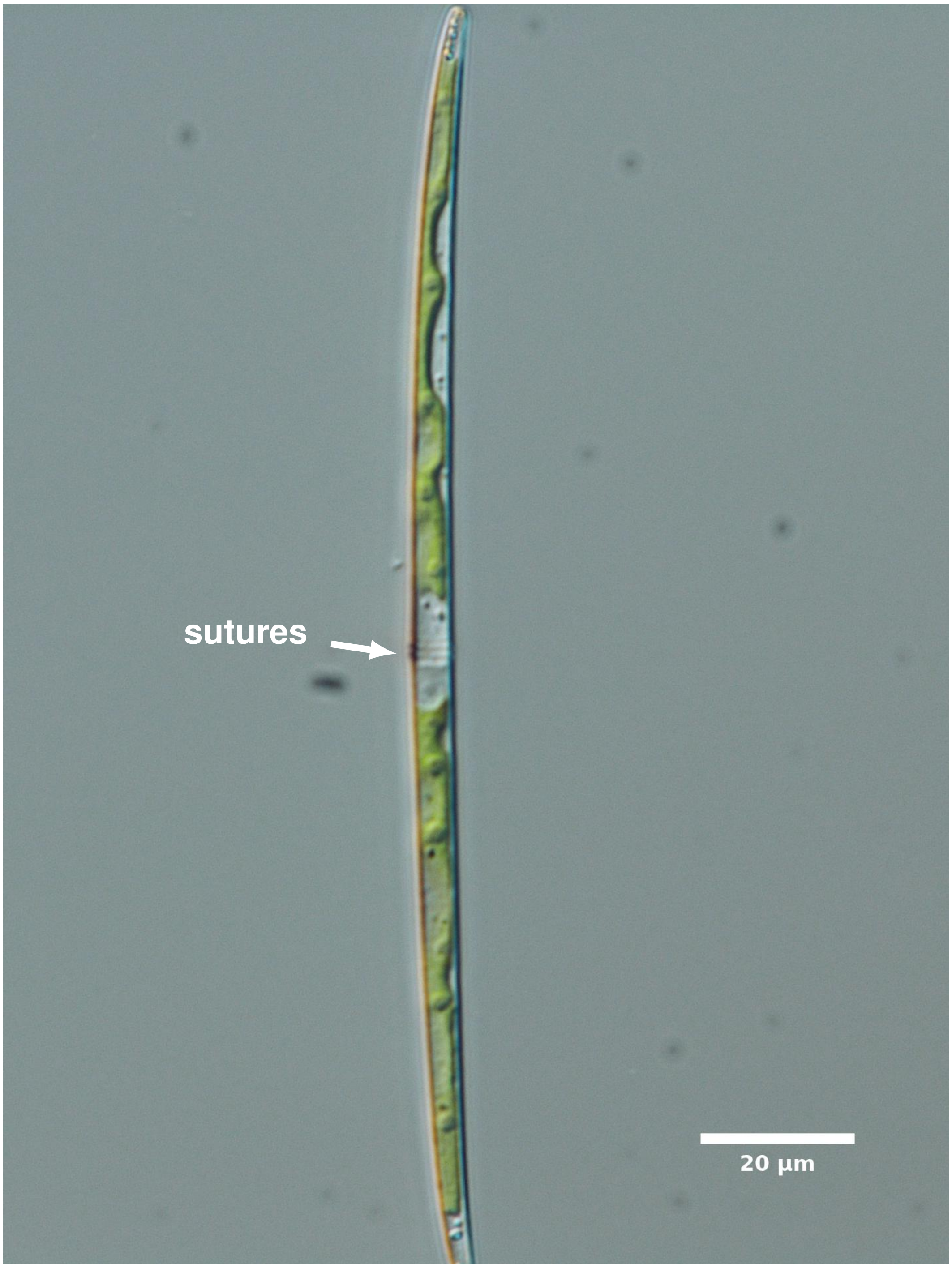


Figure 3.79: *Closterium gracile* (DIC), Lake Geneva, Whatcom County.

Figure 3.80: *Closterium gracile* f. *elongatum* (DIC), Summer Lake, Skagit County.

Figure 3.81: *Closterium gracile* f. *elongatum* (DIC), Summer Lake, Skagit County.

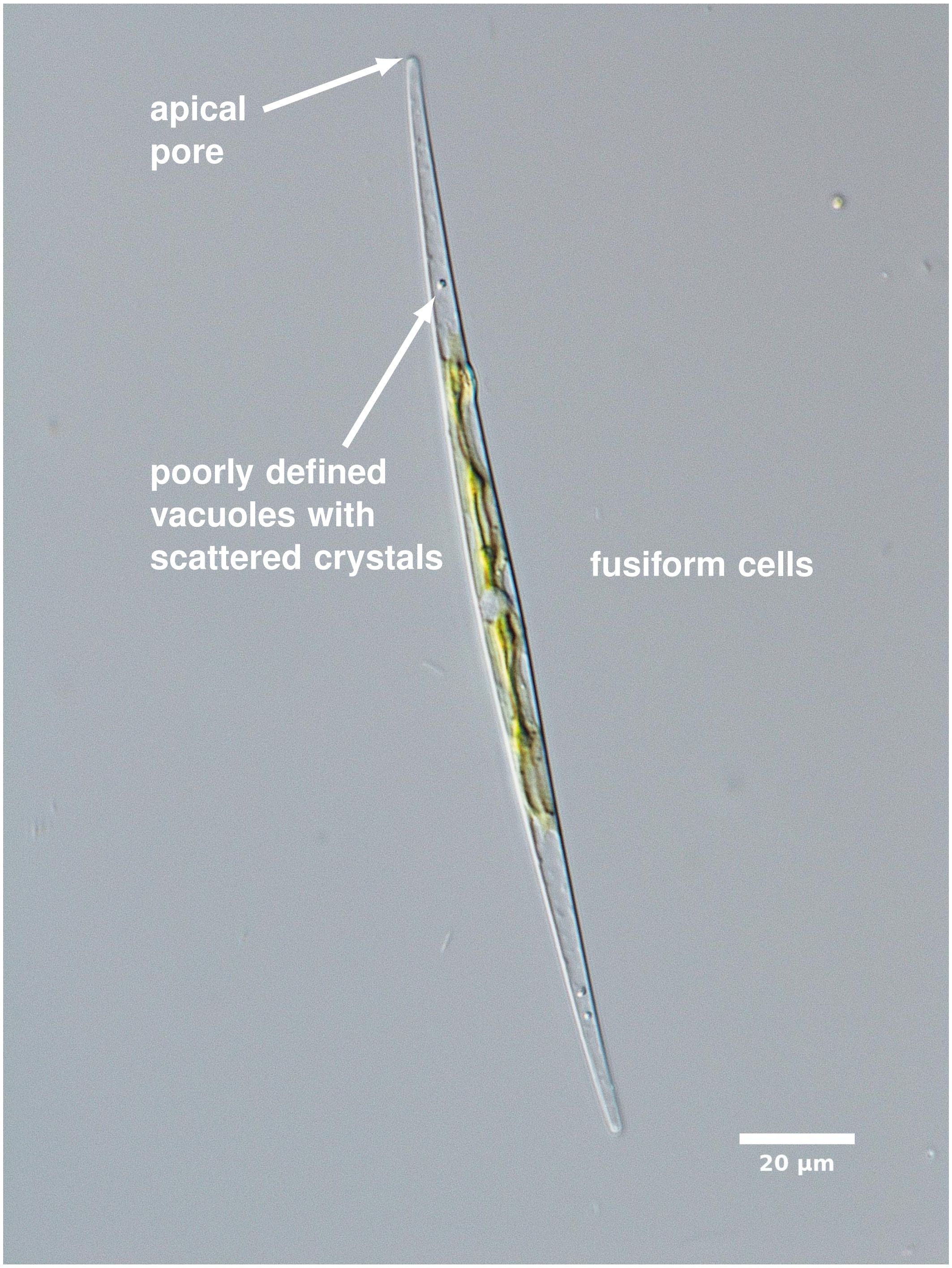


Figure 3.82: *Closterium* cf. *idiosporum* (DIC), Chain Lake, Gifford Pinchot National Forest, Skamania County.

Figure 3.83: *Closterium* cf. *idiosporum* (DIC), Summer Lake, Skagit County.

Figure 3.84: *Closterium* cf. *idiosporum* (DIC), Lake Geneva, Whatcom County.

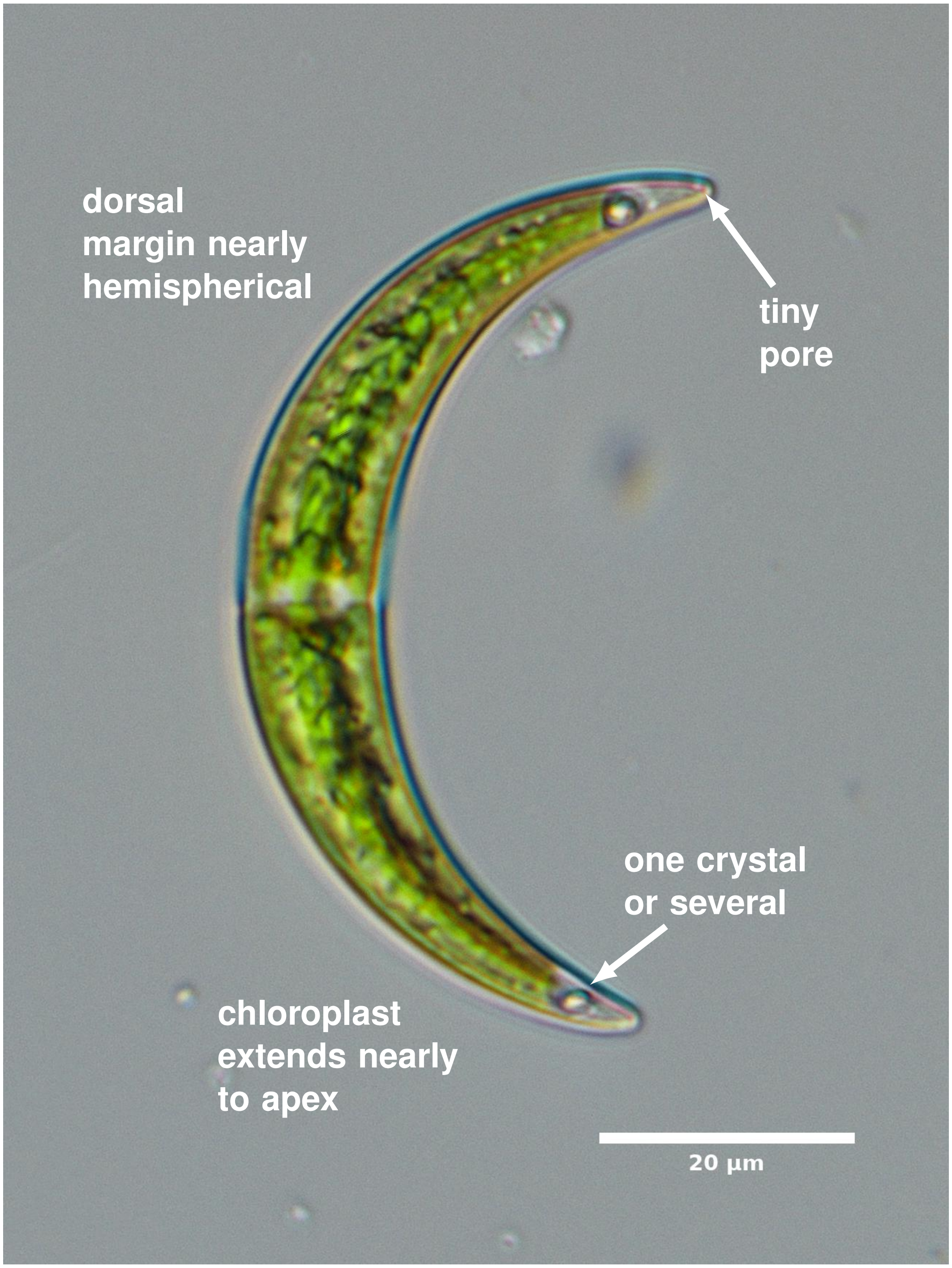


Figure 3.85: *Closterium incurvum* (DIC), small residential pond on Valley Circle Drive, Snohomish County.

Figure 3.86: *Closterium incurvum* (DIC), Beaver Lake, Skagit County.

Figure 3.87: *Closterium incurvum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.88: *Closterium incurvum* and *Closterium venus* (DIC/DIC), sample collected on same date, Hoag Pond, Whatcom County (upper/lower images).

Figure 3.89: *Closterium incurvum* var. *latius* (DIC), Cain Lake, Whatcom County.

Figure 3.90: *Closterium incurvum* var. *latius* (DIC/DIC), Grandy Lake, Skagit County (upper/lower images).

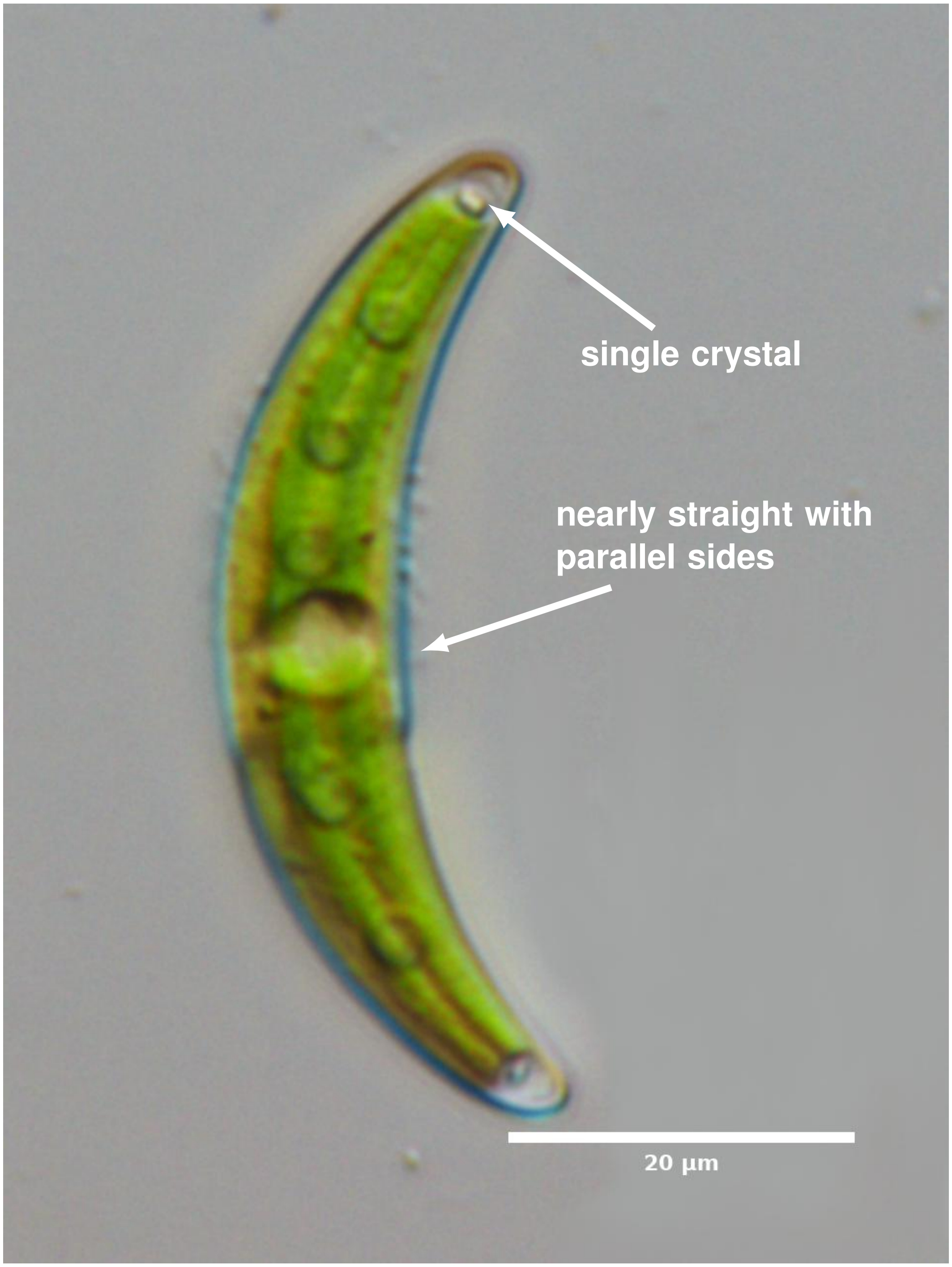


Figure 3.91: *Closterium* cf. *jenneri* var. *robustum* (DIC), small pond near Artist Point Ridge trail, Mt. Baker Recreational Area, Whatcom County.

Figure 3.92: *Closterium* cf. *jenneri* var. *robustum* (DIC), small pond near Artist Point Ridge trail, Mt. Baker area, Whatcom County.

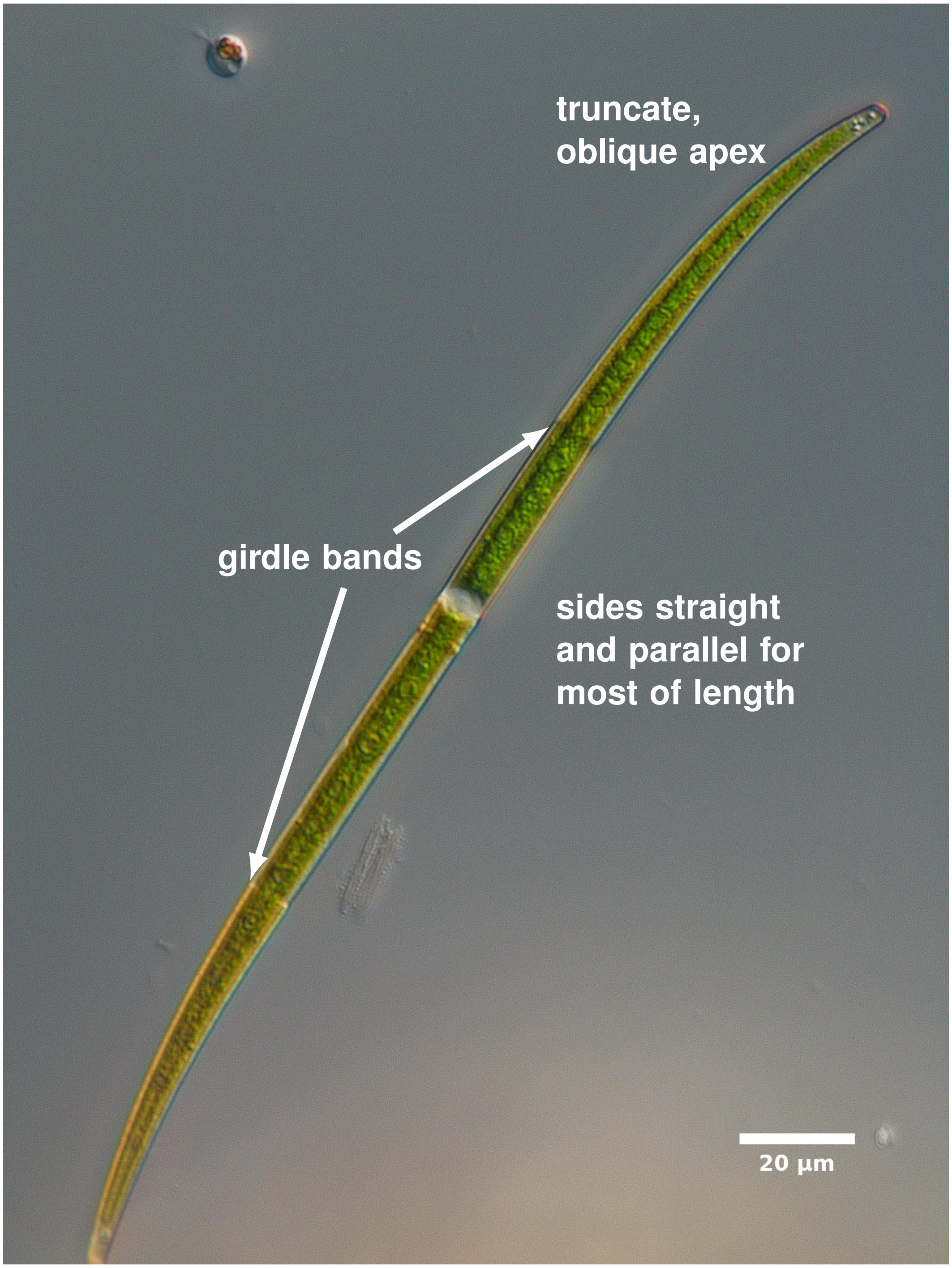


Figure 3.93: *Closterium juncidum* (DIC), Chain Lake, Gifford Pinchot National Forest, Skamania County.

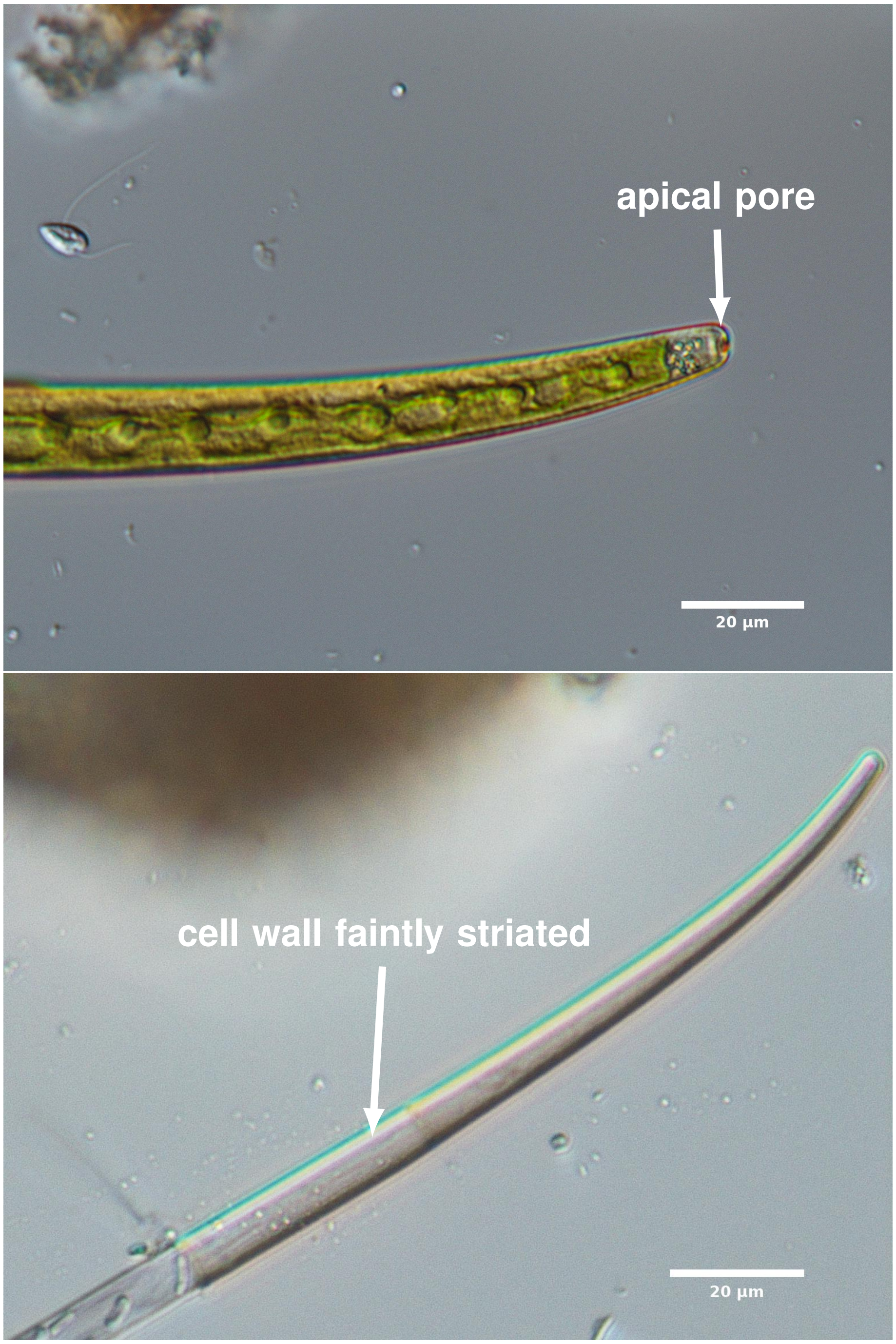


Figure 3.94: *Closterium juncidum* (DIC/DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County (upper/lower images).

Figure 3.95: *Closterium juncidum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.96: *Closterium juncidum* (DIC), small floating bog along Morris Valley Road near Harrison, BC.

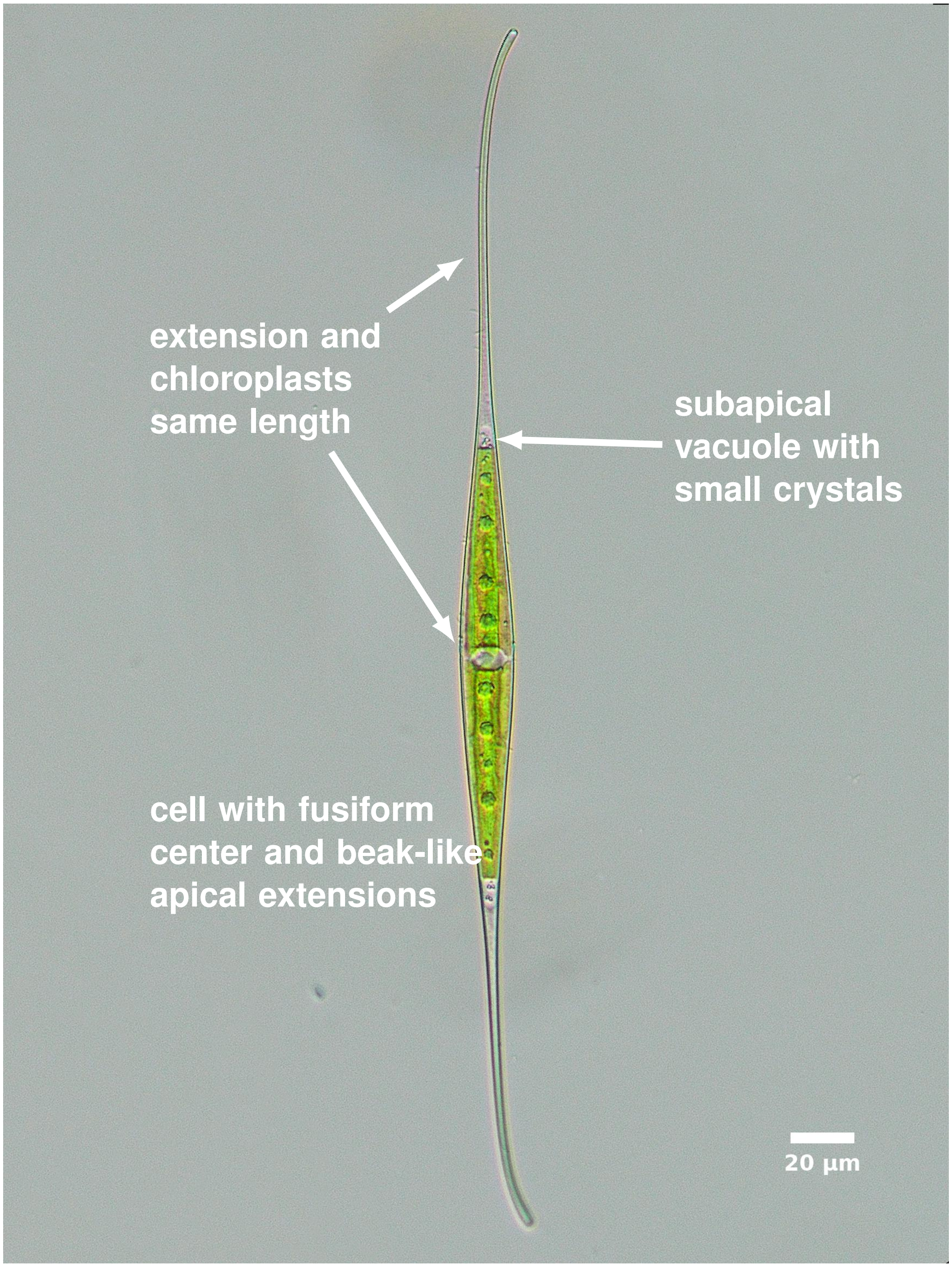


Figure 3.97: *Closterium kuetzingii* (DIC), Hoag Pond, Whatcom County.

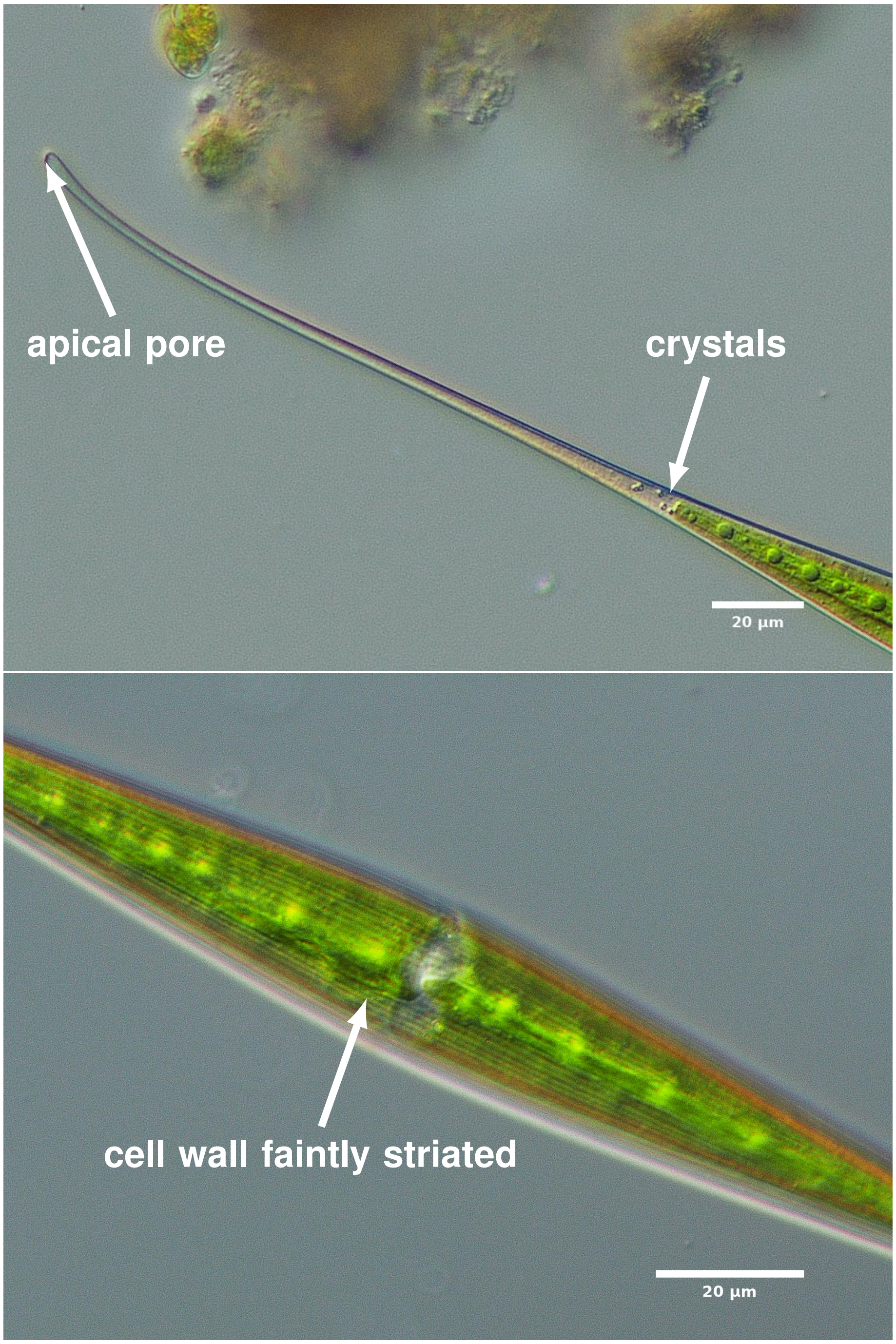


Figure 3.98: *Closterium kuetzingii* (DIC/DIC), Beaver Pond Lake, Whatcom County (upper/lower images).

Figure 3.99: *Closterium kuetzingii* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.100: *Closterium kuetzingii* (DIC), Summer Lake, Skagit County.

Figure 3.101: *Closterium kuetzingii* and *Closterium setaceum* (DIC/DIC), sample collected on same date, Summer Lake, Skagit County (upper/lower images).

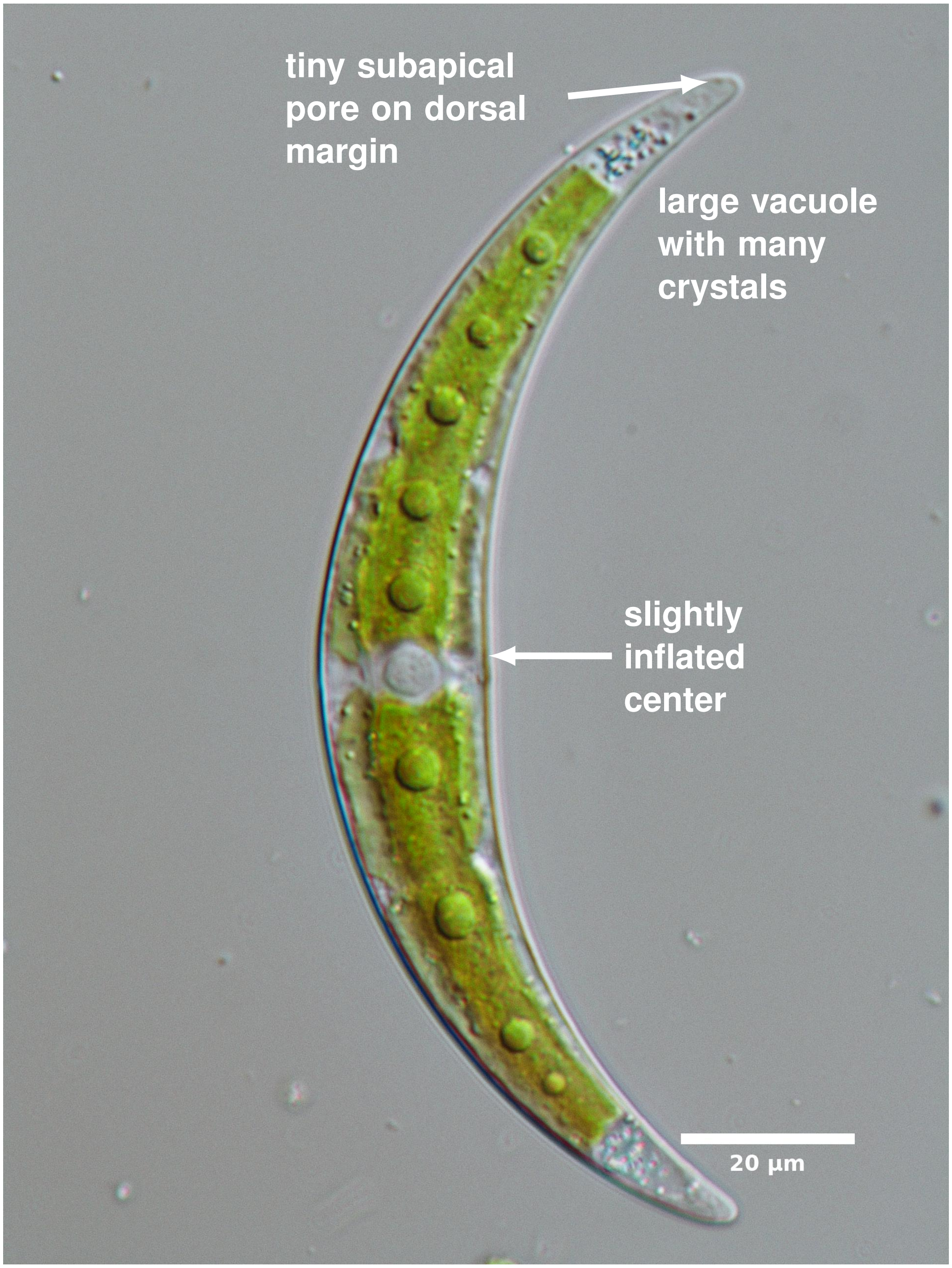


Figure 3.102: *Closterium leibleinii* (DIC), side channel on Nooksack River, Whatcom County.

Figure 3.103: *Closterium leibleinii* (DIC), side channel on Whatcom Creek, Whatcom County.

Figure 3.104: *Closterium leibleinii* (DIC), Hoag Pond, Whatcom County.

Figure 3.105: *Closterium limneticum* (DIC), Wiser Lake, Whatcom County.

Figure 3.106: *Closterium limneticum* (DIC), Wiser Lake, Whatcom County.

Figure 3.107: *Closterium limneticum* (DIC), Wiser Lake, Whatcom County.

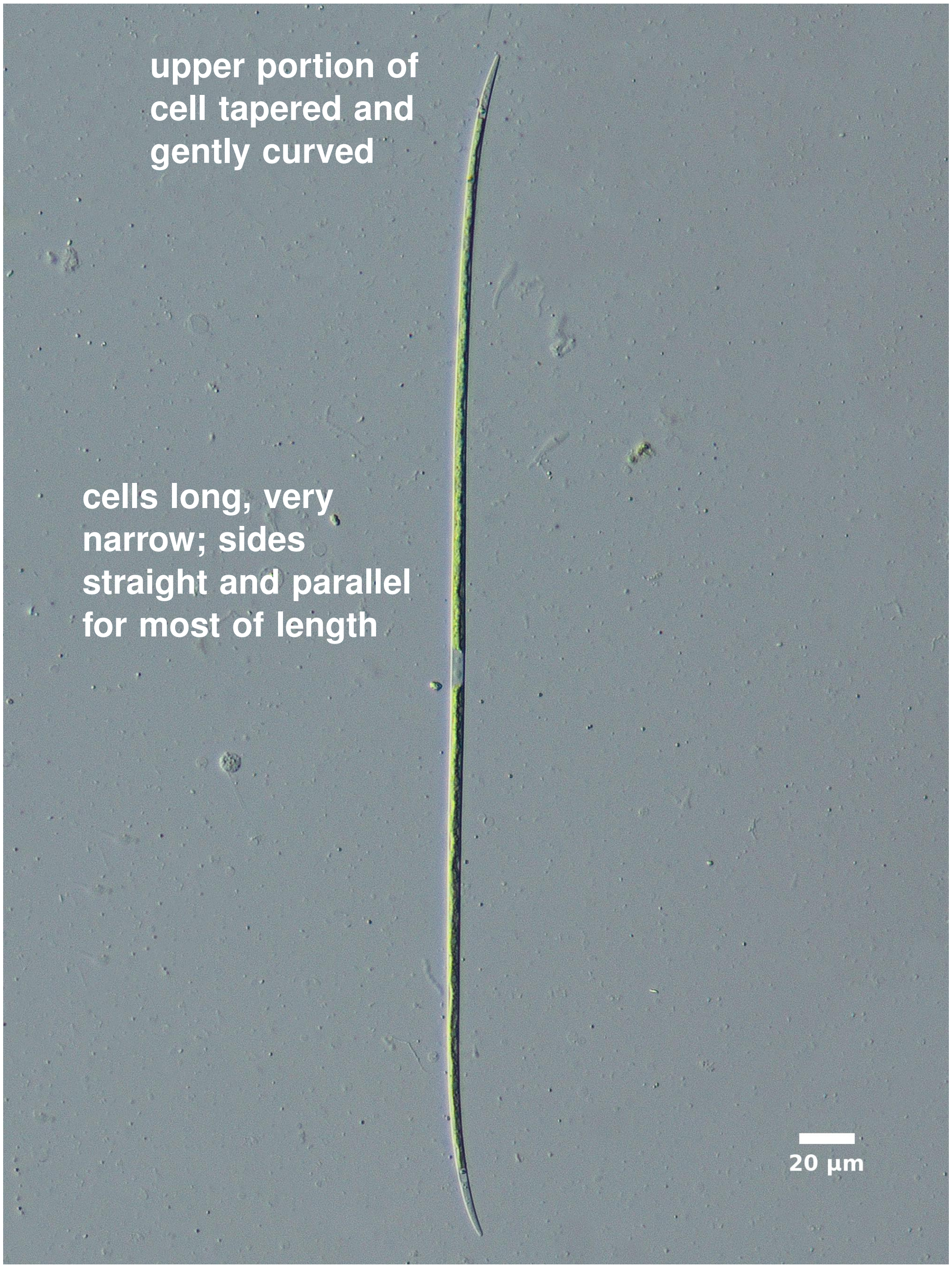


Figure 3.108: *Closterium limneticum* (DIC), Lake Terrell, Whatcom County.

Figure 3.109: *Closterium limneticum* var. *fallax* (DIC), Sunset Lake, Whatcom County.

Figure 3.110: *Closterium limneticum* var. *fallax* (DIC), Grandy Lake, Skagit County.

Figure 3.111: *Closterium limneticum* var. *fallax* (DIC), Fraser St. culvert, Bellingham, Whatcom County.

Figure 3.112: *Closterium lineatum* (DIC), Summer Lake, Skagit County.

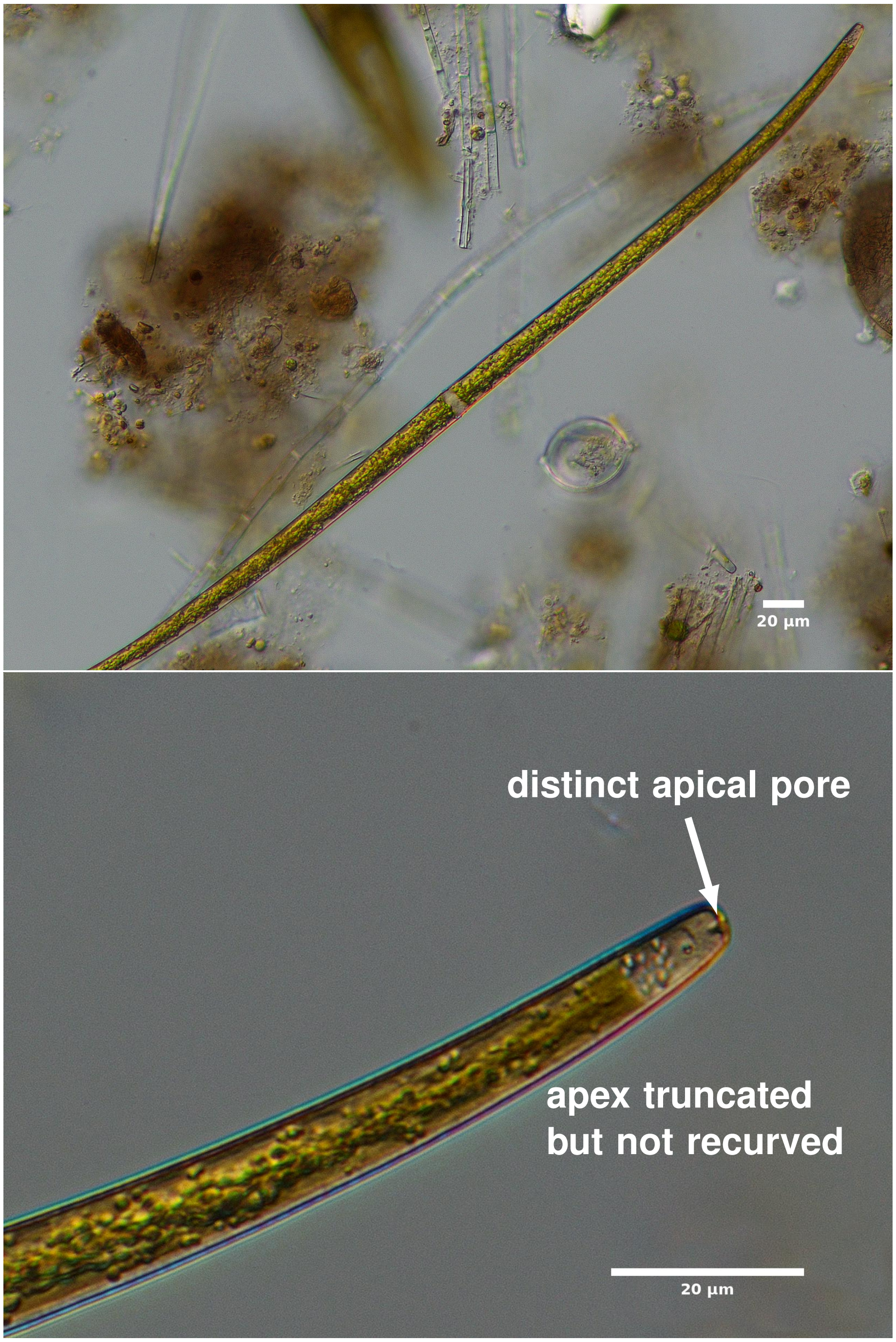


Figure 3.113: *Closterium lineatum* (DIC/DIC), Summer Lake, Skagit County (upper/lower images).

Figure 3.114: *Closterium lineatum* (DIC), Beaver Pond Lake, Whatcom County.

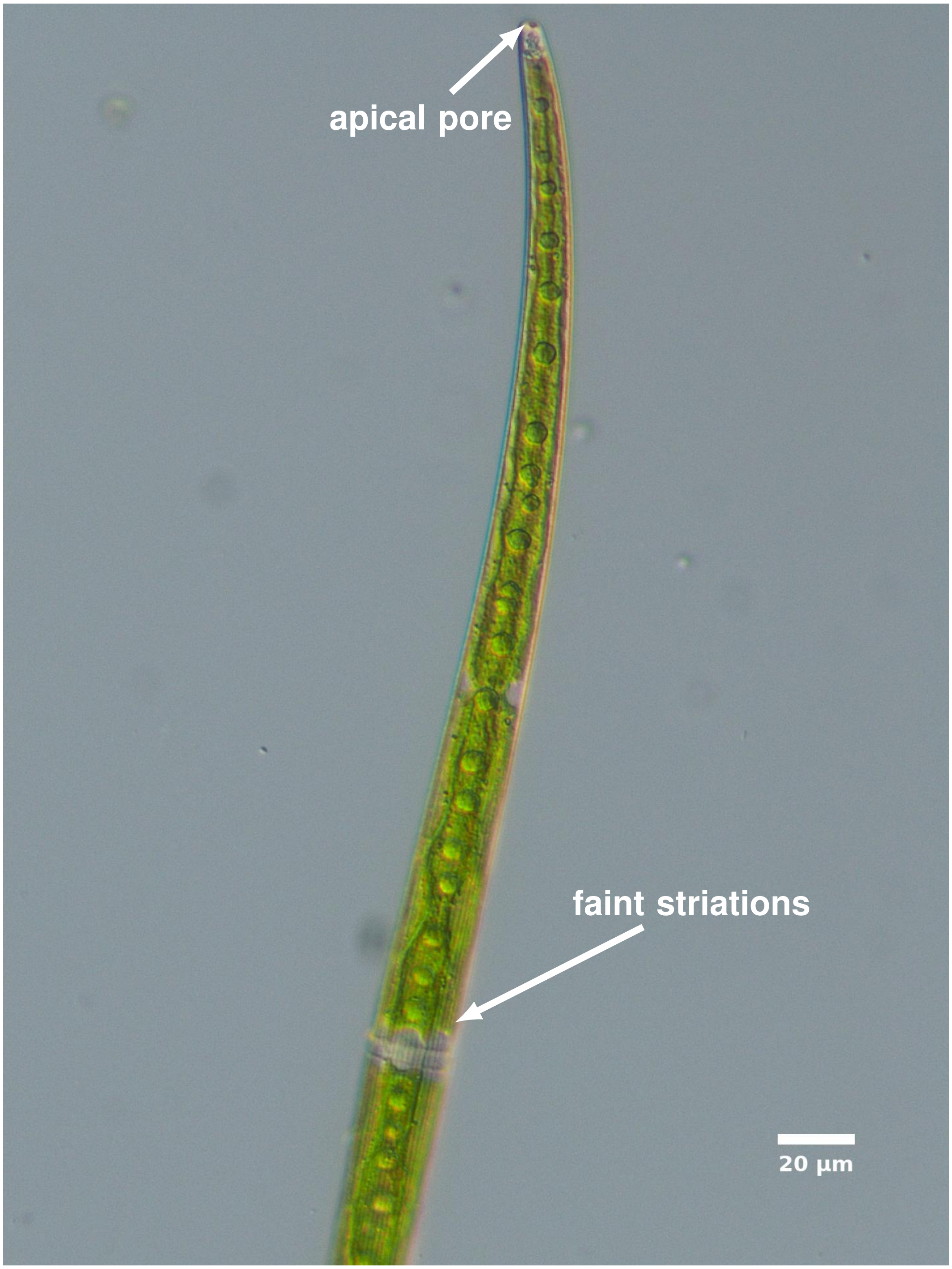


Figure 3.115: *Closterium lineatum* (DIC), Beaver Pond Lake, Whatcom County.

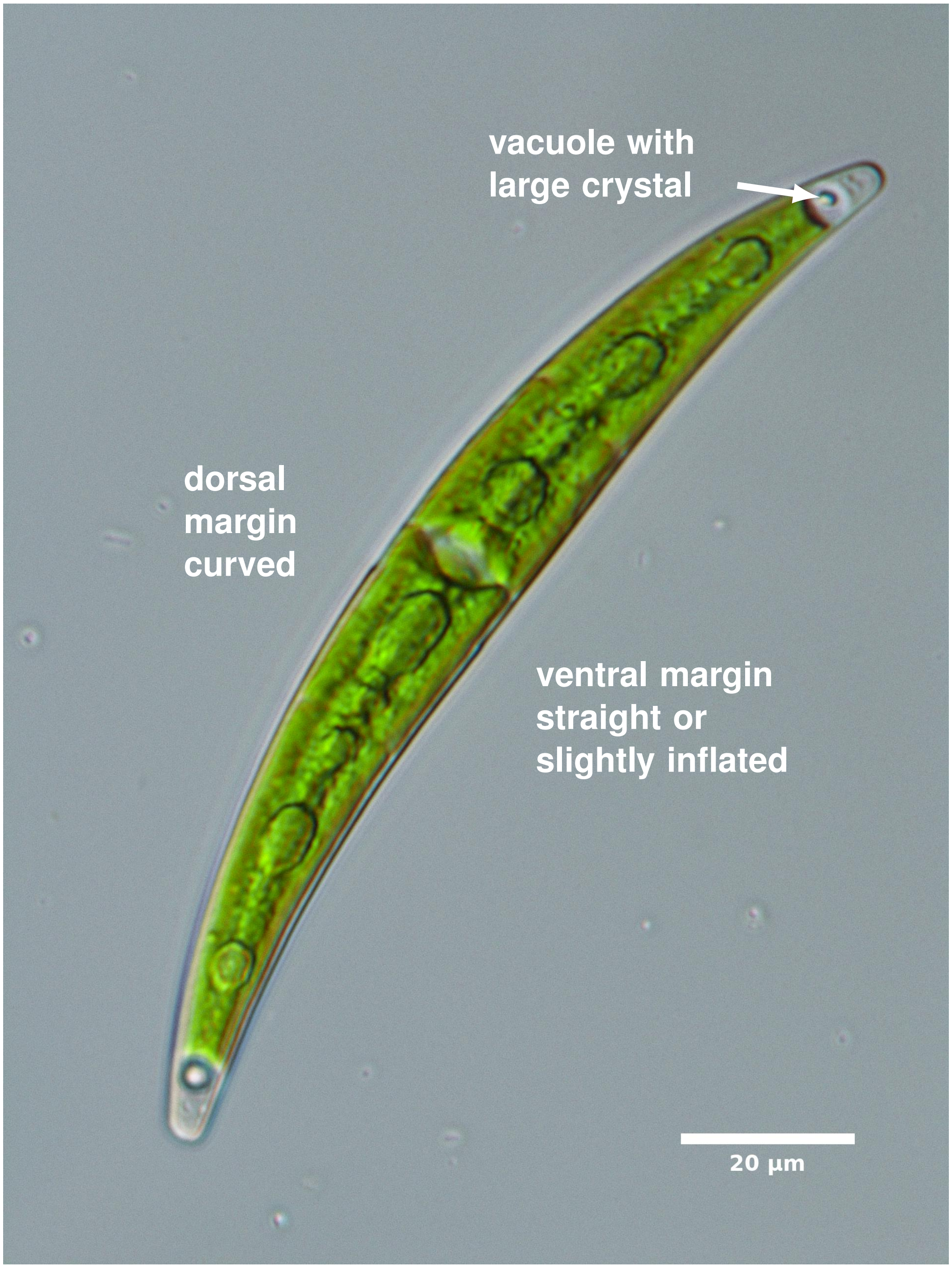


Figure 3.116: *Closterium littorale* (DIC), side channel on Chuckanut Creek, Whatcom County.

Figure 3.117: *Closterium littorale* (DIC), side channel on Nooksack River, Whatcom County.

Figure 3.118: *Closterium littorale* (DIC), small residential pond, Whatcom County.

Figure 3.119: *Closterium lunula* (DIC), Highwood Lake, Mt. Baker area, Whatcom County.

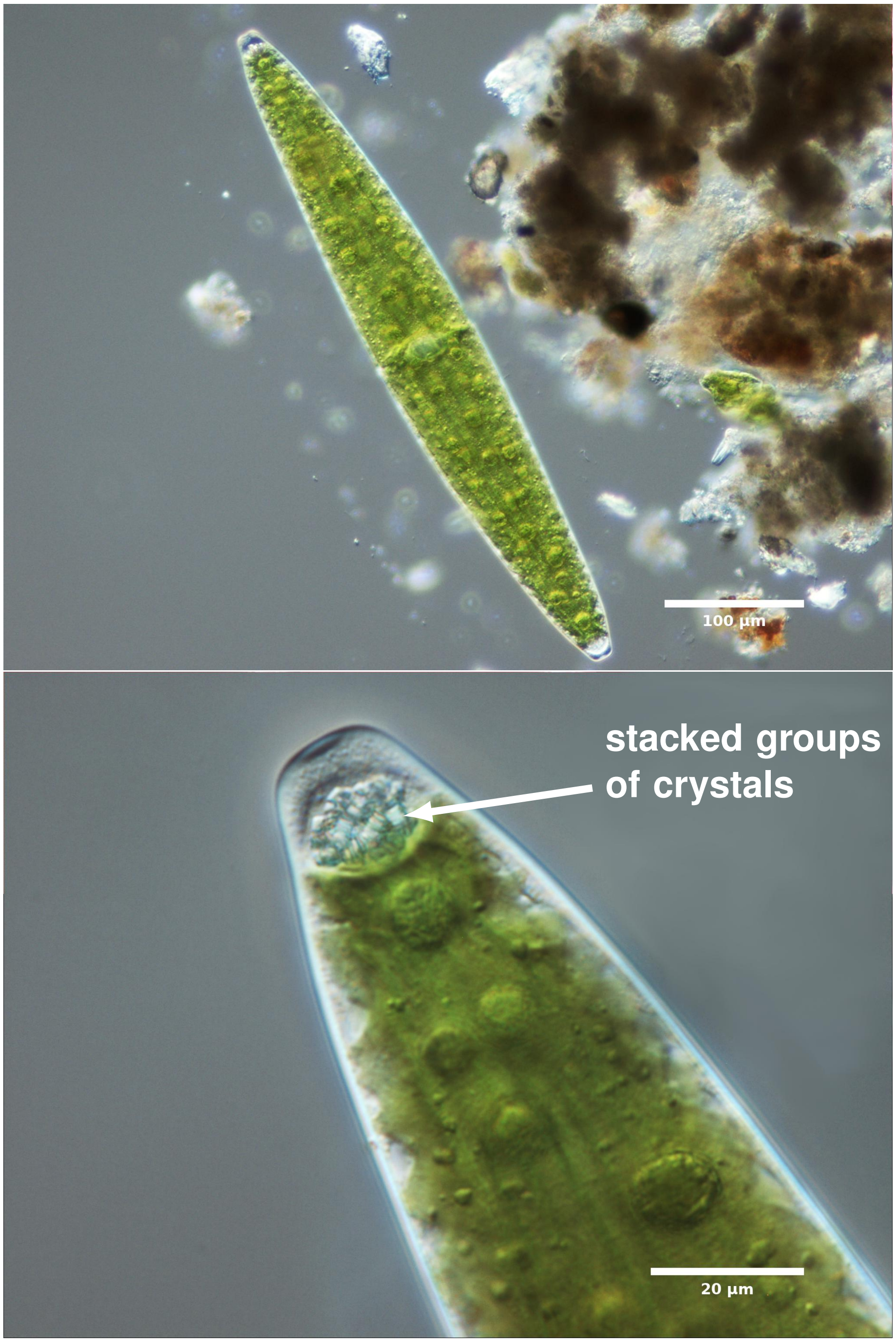


Figure 3.120: *Closterium lunula* (DIC/DIC), Highwood Lake, Mt. Baker area, Whatcom County (upper/lower images).

Figure 3.121: *Closterium lunula* (DIC/DIC), Mirror Lake, Whatcom County (upper/lower images).

Figure 3.122: *Closterium lunula* (DIC), small floating bog along Morris Valley Road near Harrison, BC.

Figure 3.123: *Closterium lunula* (DIC), Lower Ashland Lake, Mountain Loop Highway, Snohomish County.

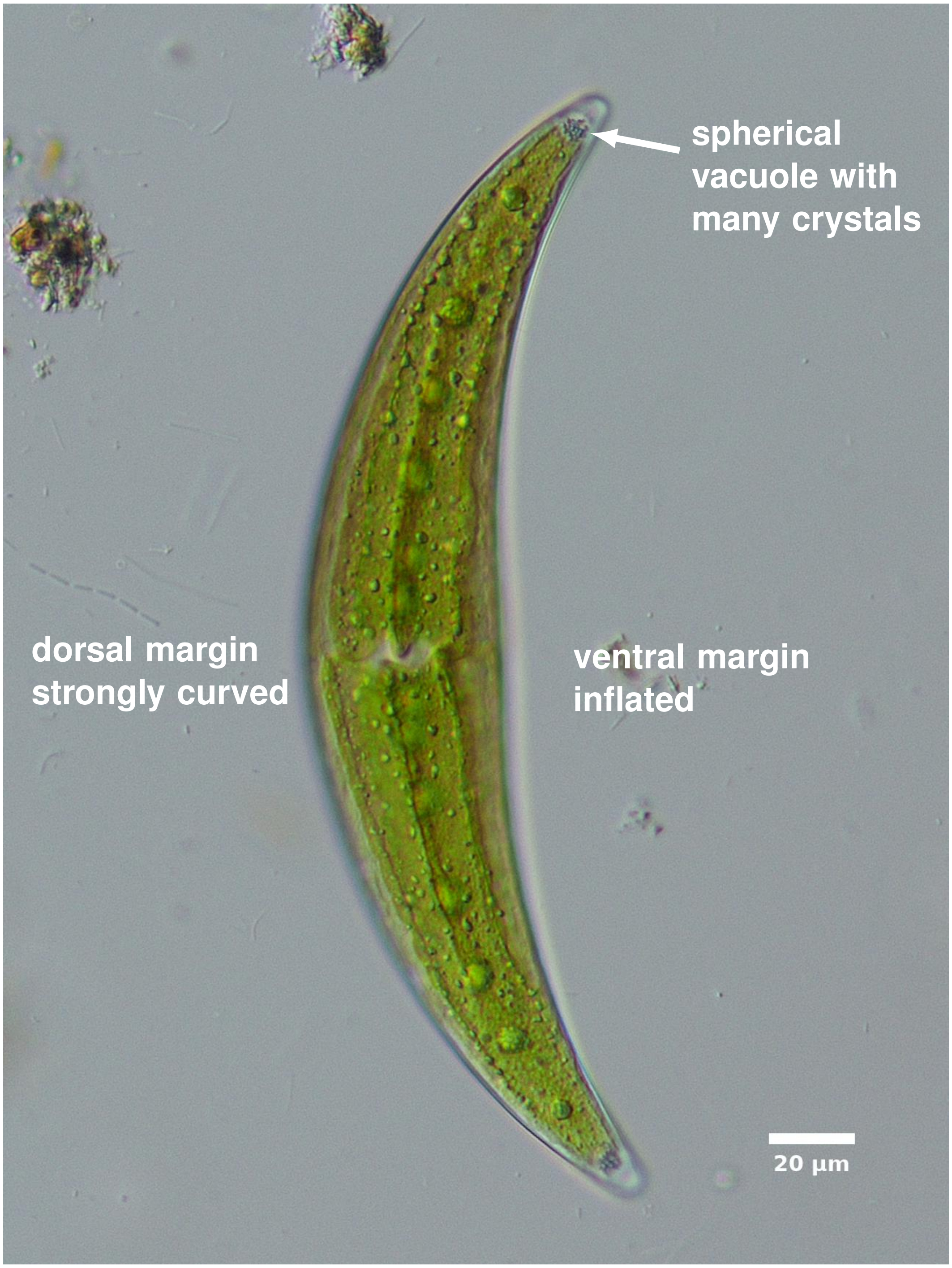


Figure 3.124: *Closterium moniliferum*), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.125: *Closterium moniliferum* (DIC/DIC), Lake Campbell (eastern Washington), Okanogan County (upper image); Squalicum Lake, Whatcom County (lower image).

Figure 3.126: *Closterium moniliferum*), Beaver Pond Lake, Whatcom County.

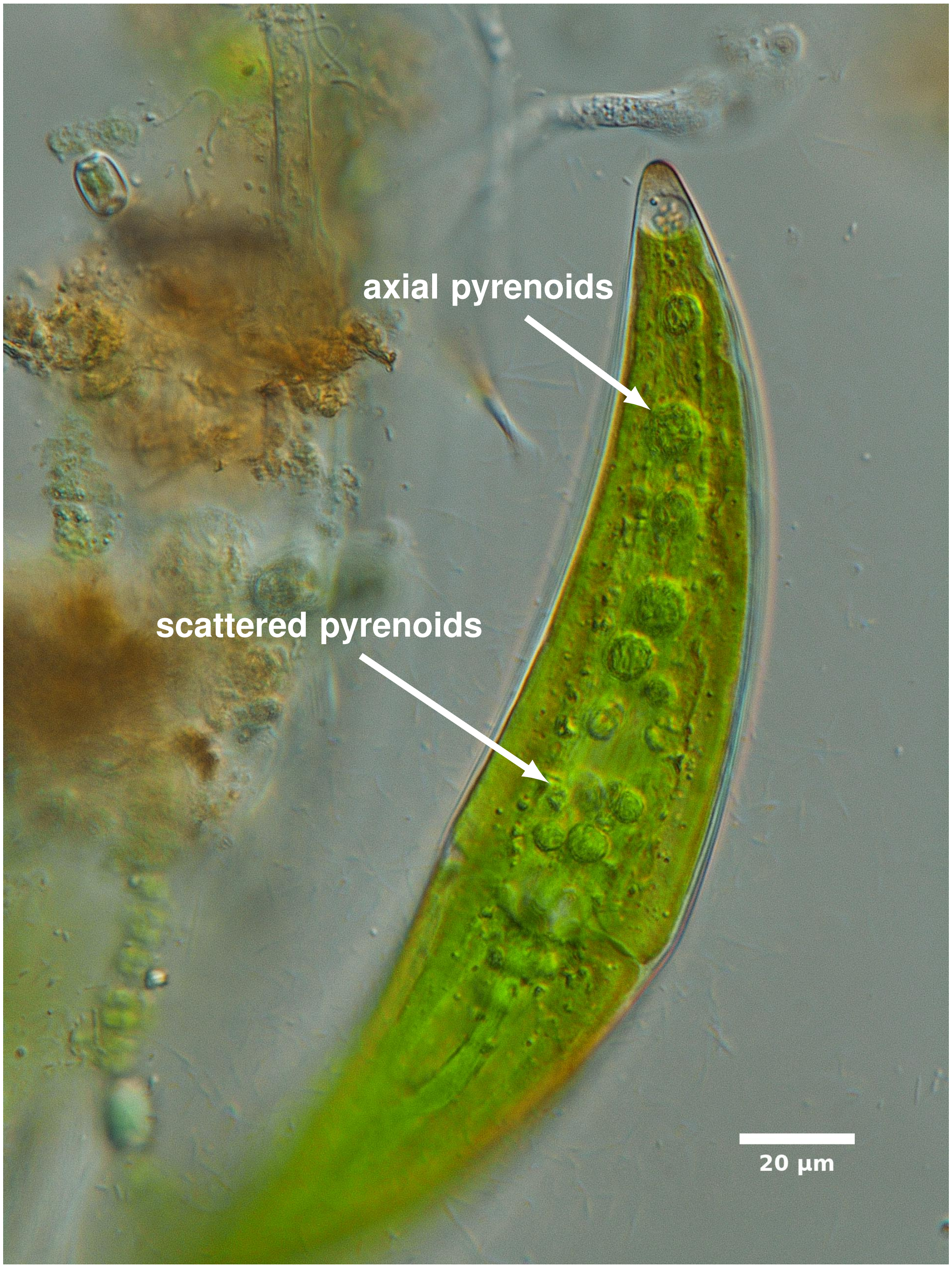


Figure 3.127: *Closterium moniliferum*) with axial and scattered pyrenoids, Lake Geneva, Whatcom County.

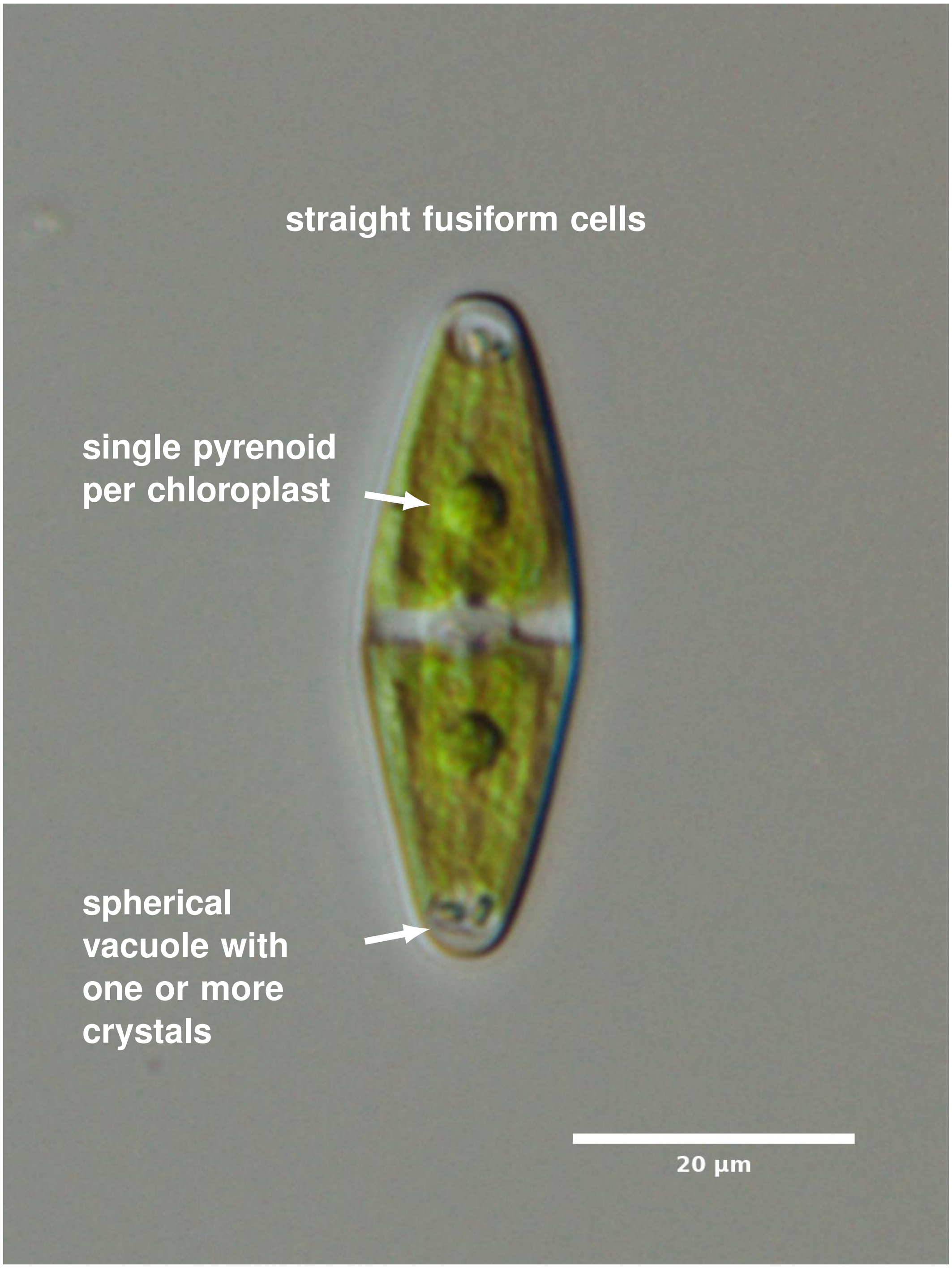


Figure 3.128: *Closterium navicula* (DIC), small pond near Artist Point Ridge trail, Mt. Baker Recreational Area, Whatcom County.

Figure 3.129: *Closterium navicula* (DIC), side channel on Nooksack River, Whatcom County.

Figure 3.130: *Closterium navicula* (DIC), small pond on trail to Big Four Ice Caves, Mountain Loop Highway, Snohomish County.

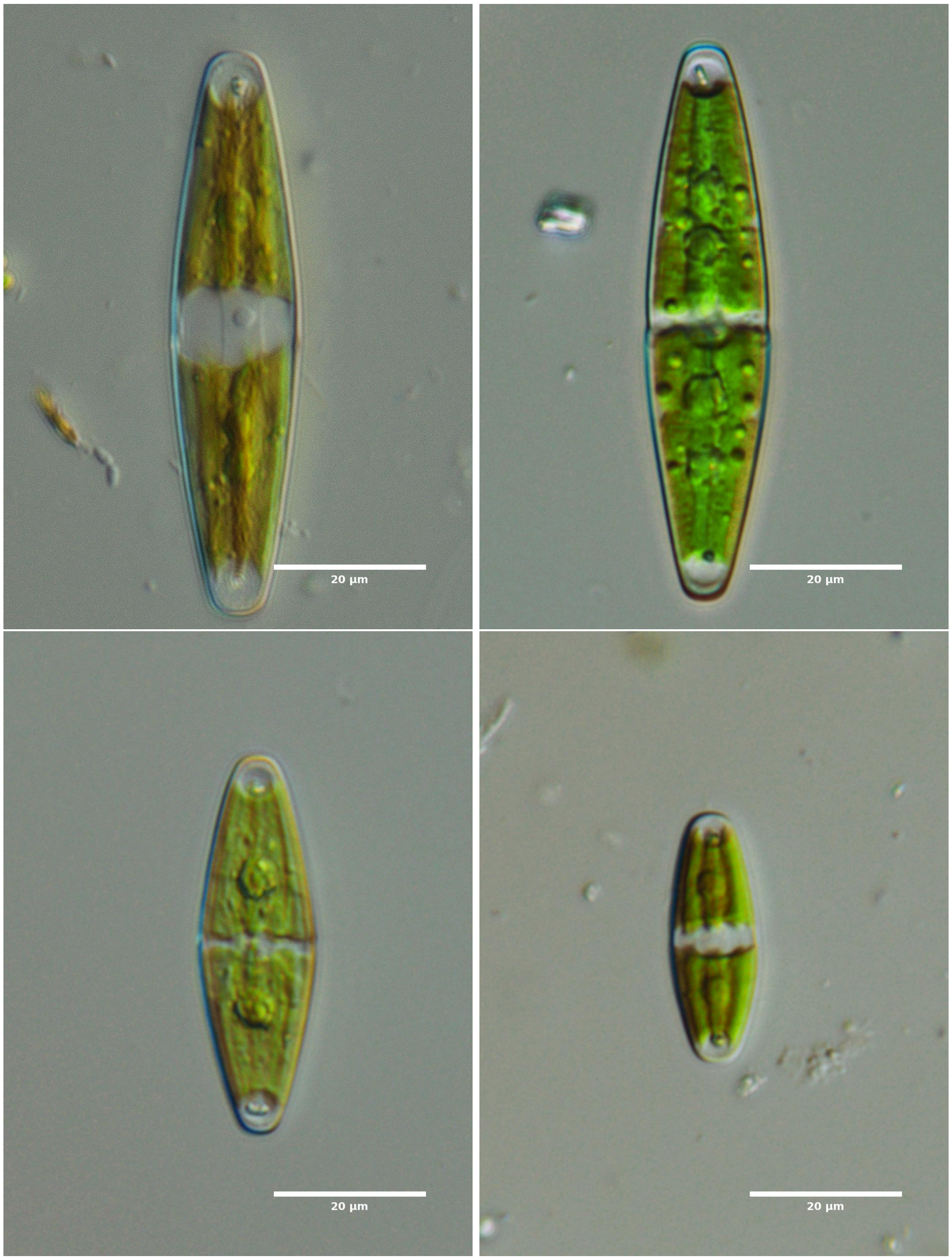


Figure 3.131: Size variations in *Closterium navicula* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County (upper left image); small pond along Artist Point Ridge trail, Mt. Baker area, Whatcom County (upper right and lower left images); small pond on trail to Dock Butte, Mt. Baker area, Skagit County (lower right image).

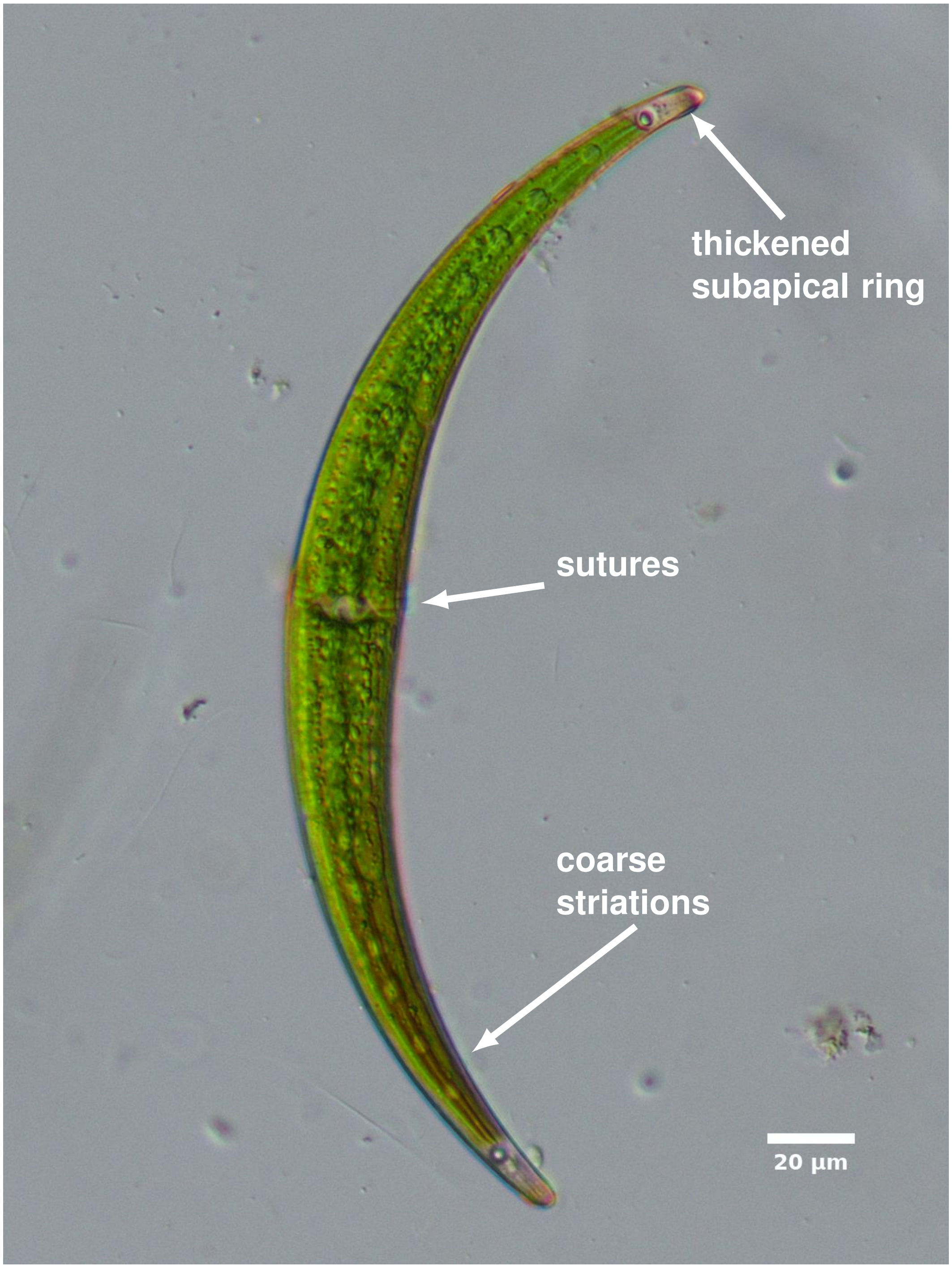


Figure 3.132: *Closterium nematodes* (DIC), Upper Ashland Lake, Mountain Loop Highway, Snohomish County.

Figure 3.133: *Closterium nematodes* (DIC), Upper Ashland Lake, Mountain Loop Highway, Snohomish County.

Figure 3.134: *Closterium nematodes* (DIC), Bear Lake, Mountain Loop Highway, Snohomish County.

Figure 3.135: *Closterium nematodes* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

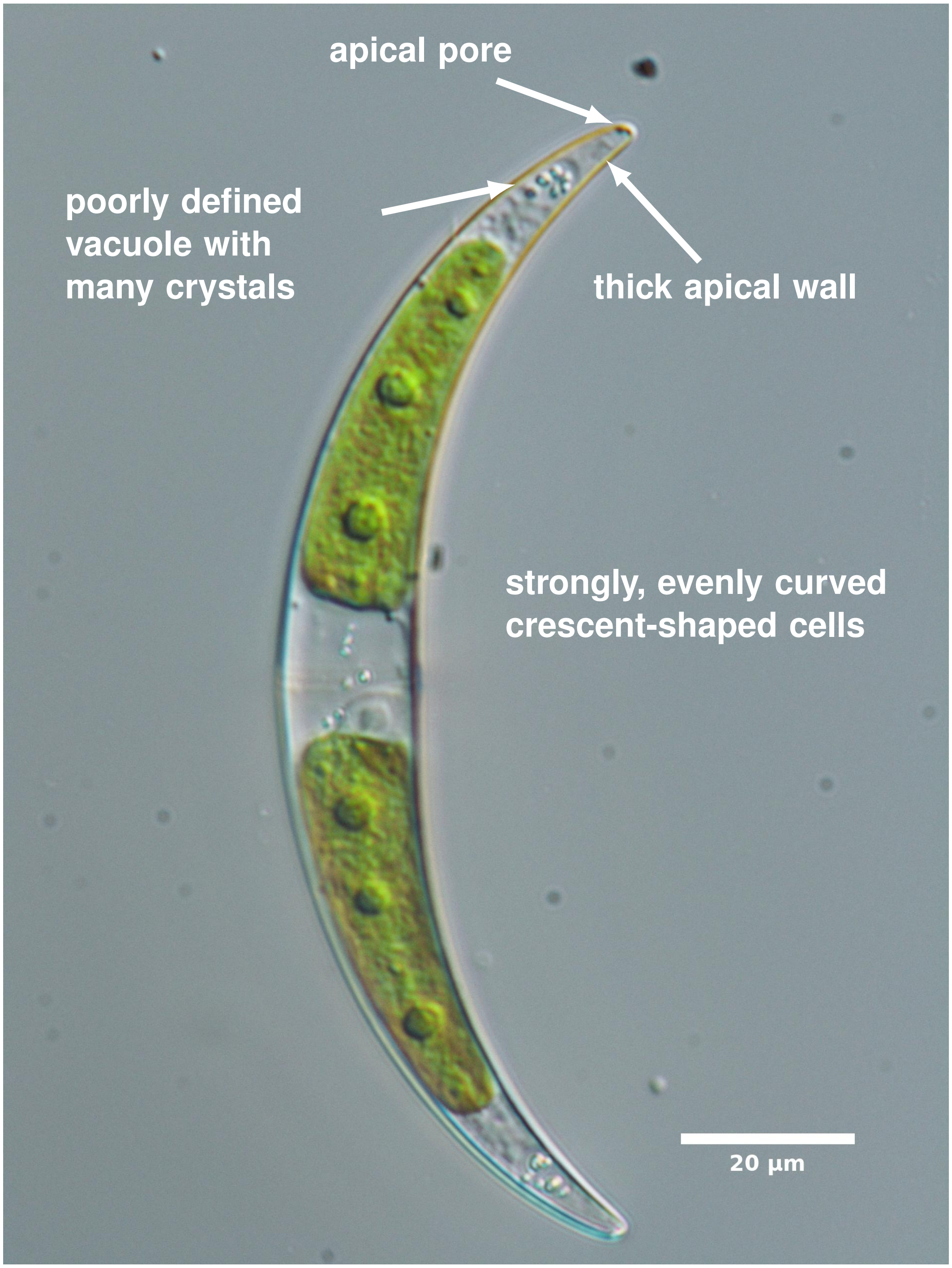


Figure 3.136: *Closterium parvulum* (DIC), Beaver Pond Lake, Whatcom County.

Figure 3.137: *Closterium parvulum* (DIC/DIC), Squalicum Lake, Whatcom County (upper/lower images).

Figure 3.138: *Closterium parvulum* (DIC), Pine Lake, Whatcom County.

Figure 3.139: *Closterium parvulum* group var. A (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.140: *Closterium parvulum* group var. A (DIC), Beaver Pond Lake, Whatcom County.

Figure 3.141: *Closterium parvulum* group var. A (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.142: *Closterium parvulum* group var. B (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.143: *Closterium parvulum* group var. B (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.144: *Closterium praelongum* (DIC), Lake Ketchum, Snohomish County.

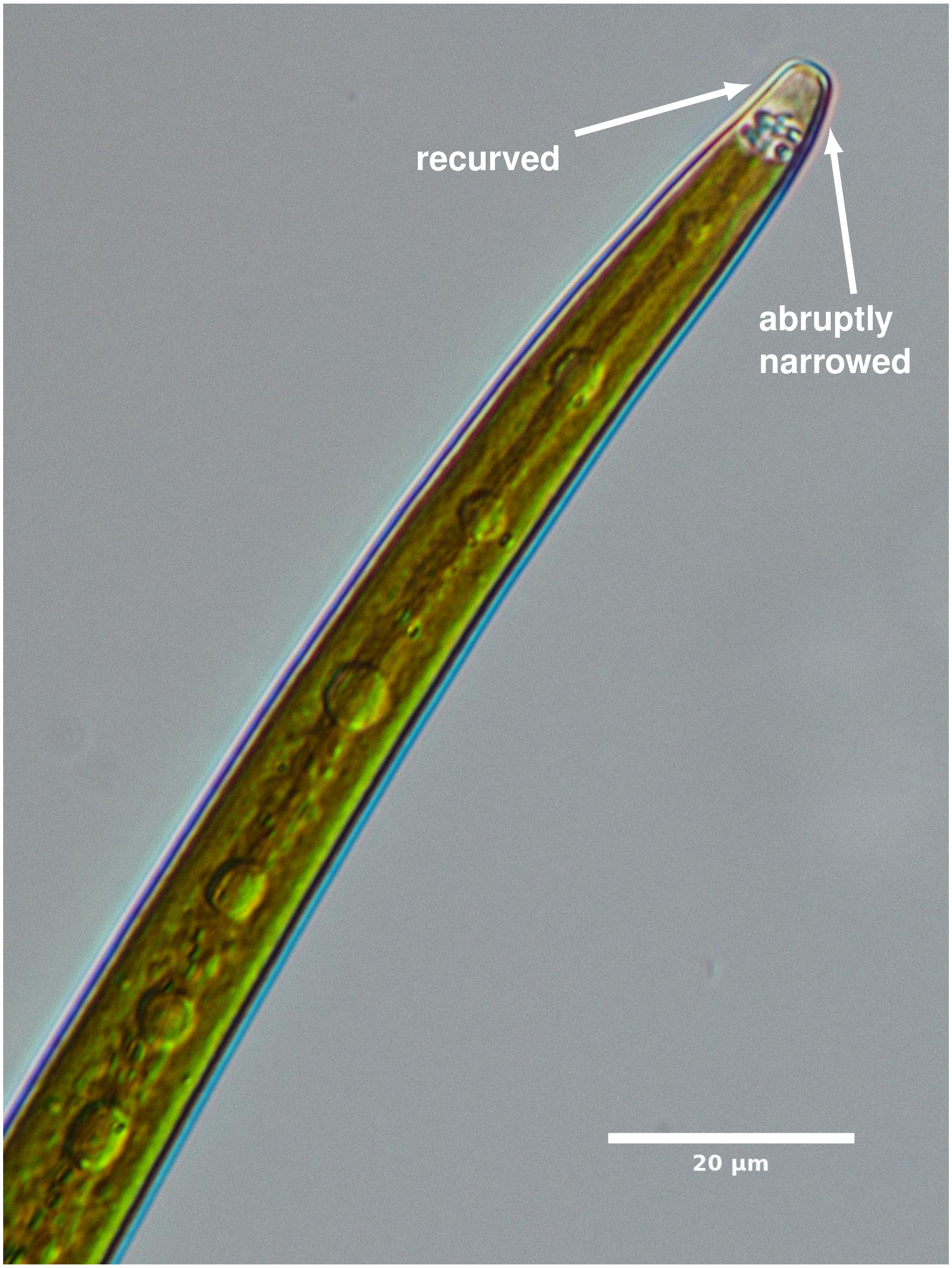


Figure 3.145: *Closterium praelongum* (DIC), Lake Ketchum, Snohomish County.

Figure 3.146: *Closterium praelongum* (DIC), Fraser St. culvert, Bellingham, Whatcom County.

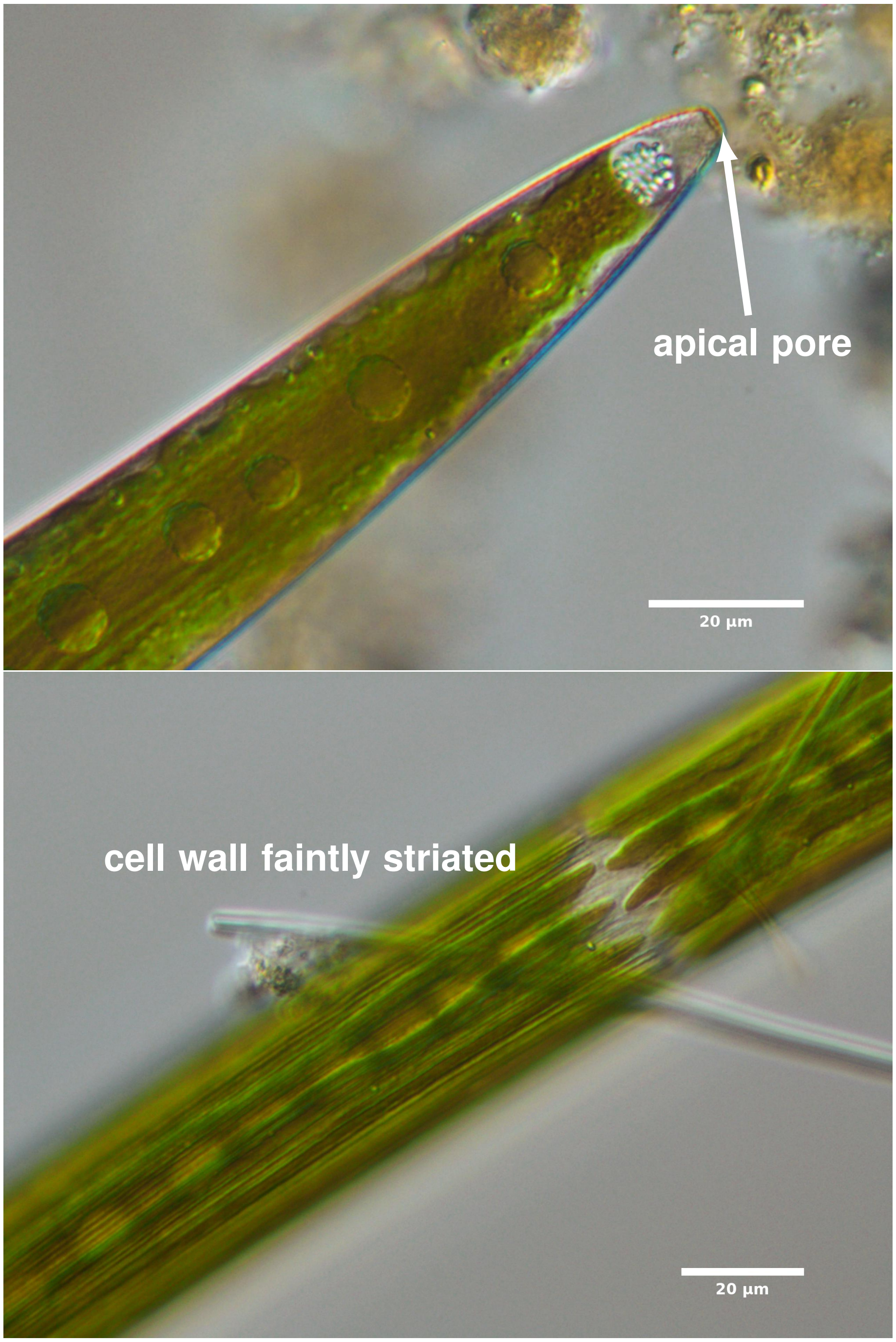


Figure 3.147: *Closterium praelongum* (DIC/DIC), Fraser St. culvert, Bellingham, Whatcom County (upper/lower images).

Figure 3.148: *Closterium pritchardianum* (DIC), Vogler Lake, Skagit County.

Figure 3.149: *Closterium pritchardianum* (DIC/DIC), Vogler Lake, Skagit County (upper/lower images).

Figure 3.150: *Closterium pronum* (DIC), Lake Campbell (eastern Washington), Okanogan County.

Figure 3.151: *Closterium pronum* (DIC), Lake Terrell, Whatcom County.

Figure 3.152: *Closterium pronum* (DIC), small floating bog along Morris Valley Road near Harrison, BC.

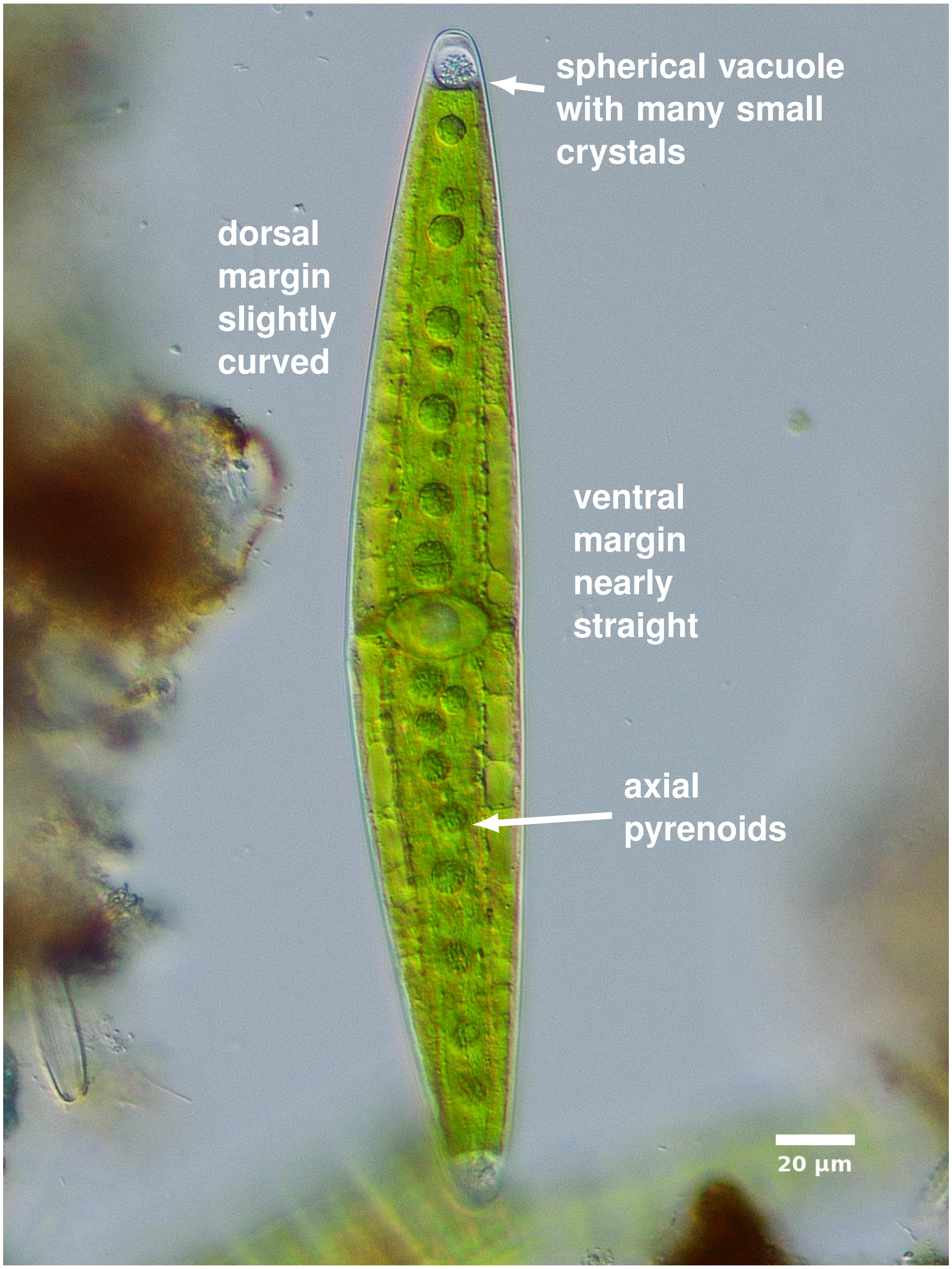


Figure 3.153: *Closterium pseudolunula* (DIC), small pond along Military Road south of Tacoma, Pierce County.

Figure 3.154: *Closterium pseudolunula* (DIC), Lake Sixteen, Skagit County.

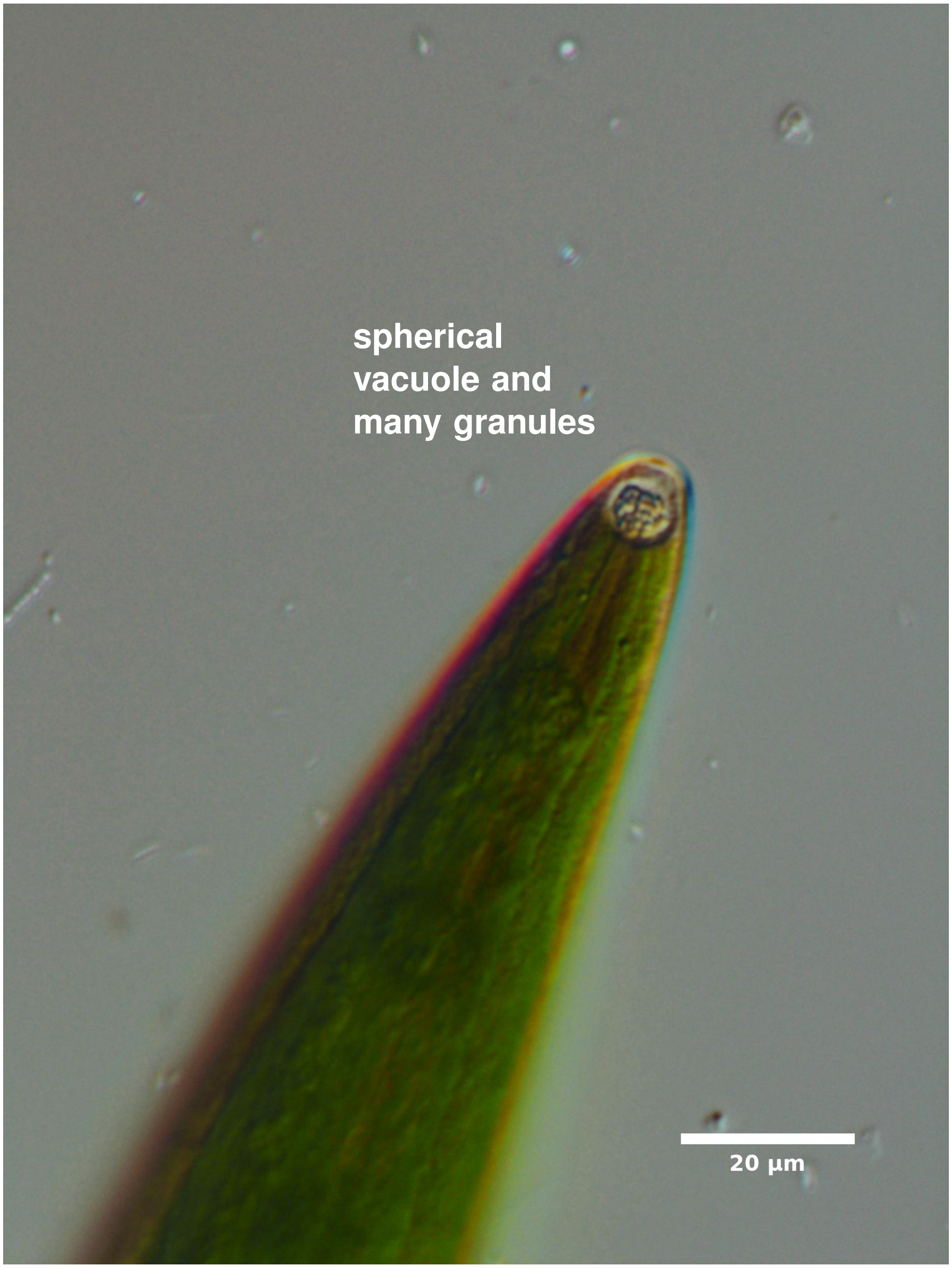


Figure 3.155: *Closterium pseudolunula* (DIC), Lake Sixteen, Skagit County.

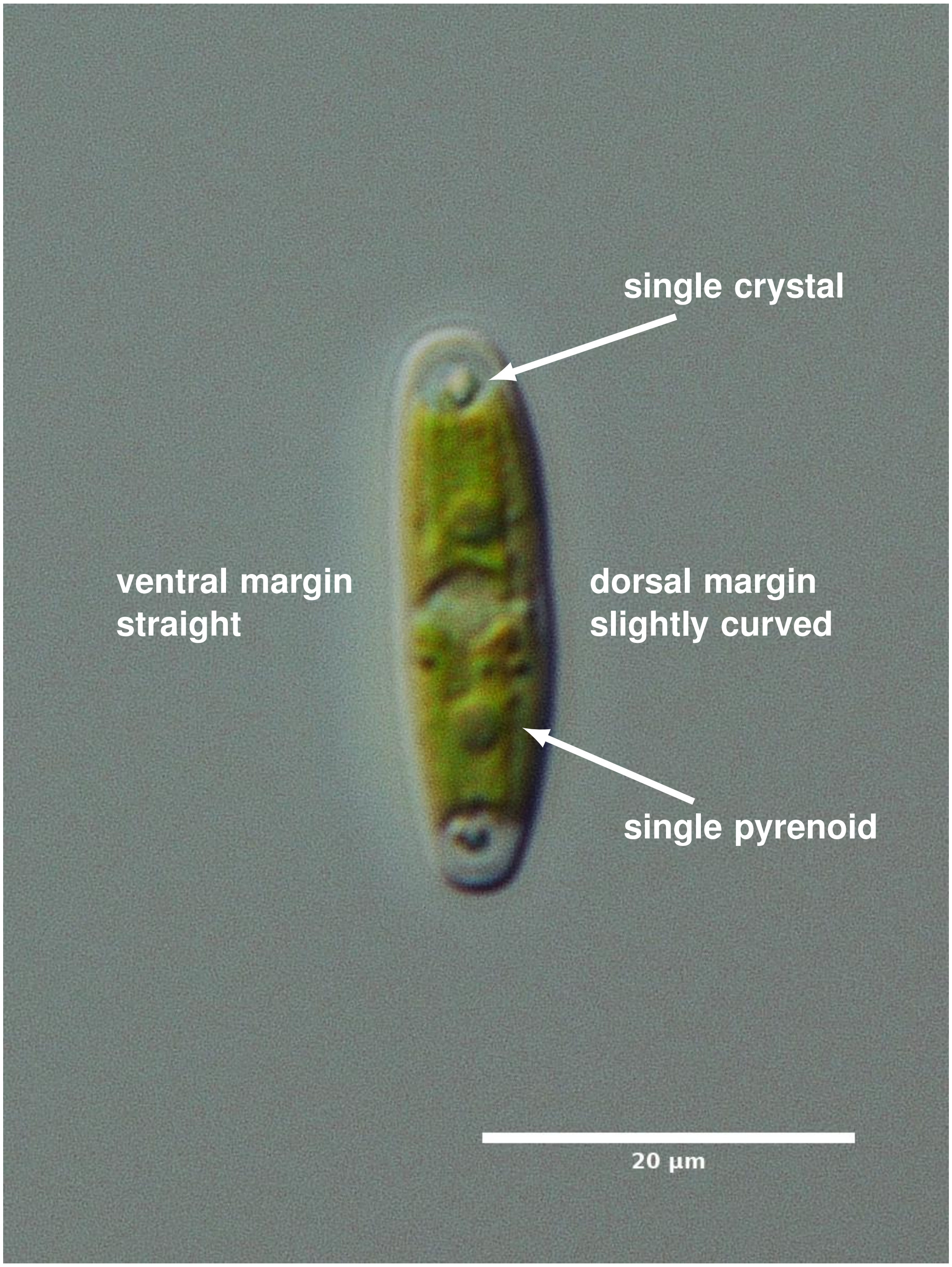


Figure 3.156: *Closterium pusillum* (DIC), Takhlakh Lake, Gifford Pinchot National Forest, Skamania County.

Figure 3.157: *Closterium pusillum* (bright field), Vogler Lake, Skagit County.

Figure 3.158: *Closterium pusillum* (DIC), Takhlakh Lake, Gifford Pinchot National Forest, Skamania County.

Figure 3.159: *Closterium pusillum* (DIC/DIC), Takhlakh Lake, Gifford Pinchot National Forest, Skamania County (upper/lower images).

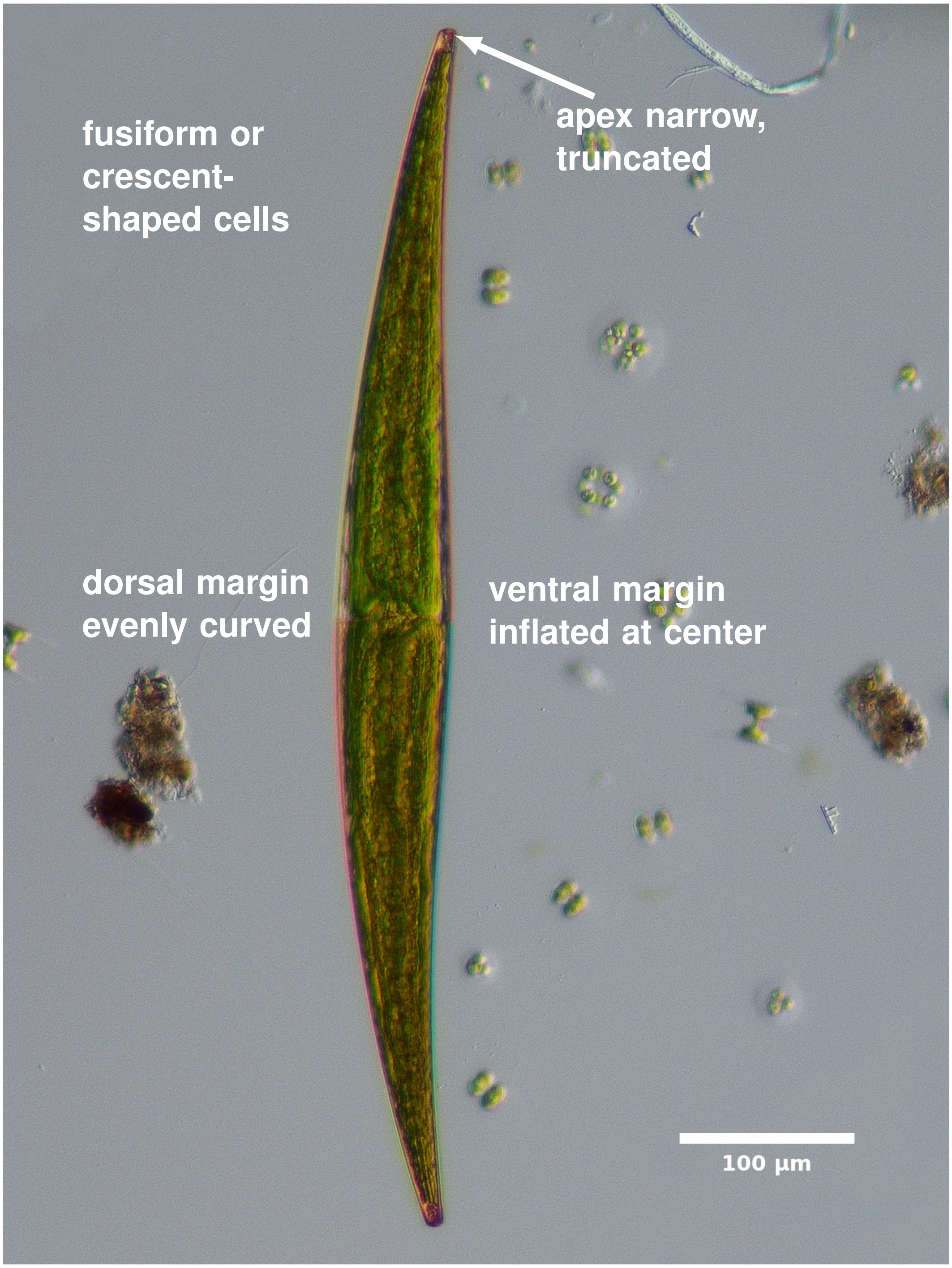


Figure 3.160: *Closterium ralfsii* var. *hybridum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.161: *Closterium ralfsii* var. *hybridum* (DIC), Mirror Lake, Whatcom County.

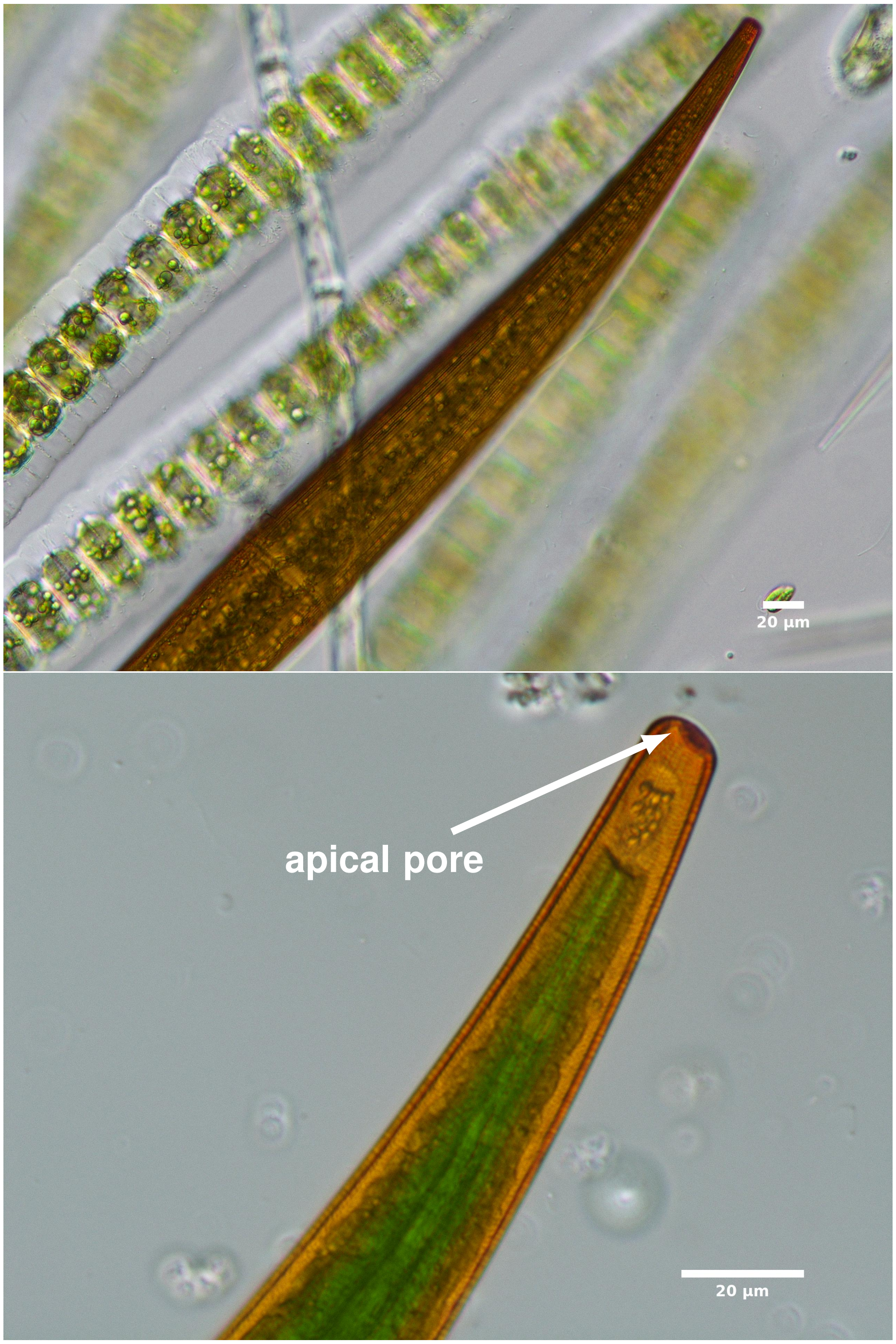


Figure 3.162: *Closterium ralfsii* var. *hybridum* (DIC/DIC), Summer Lake, Skagit County (upper/lower images).

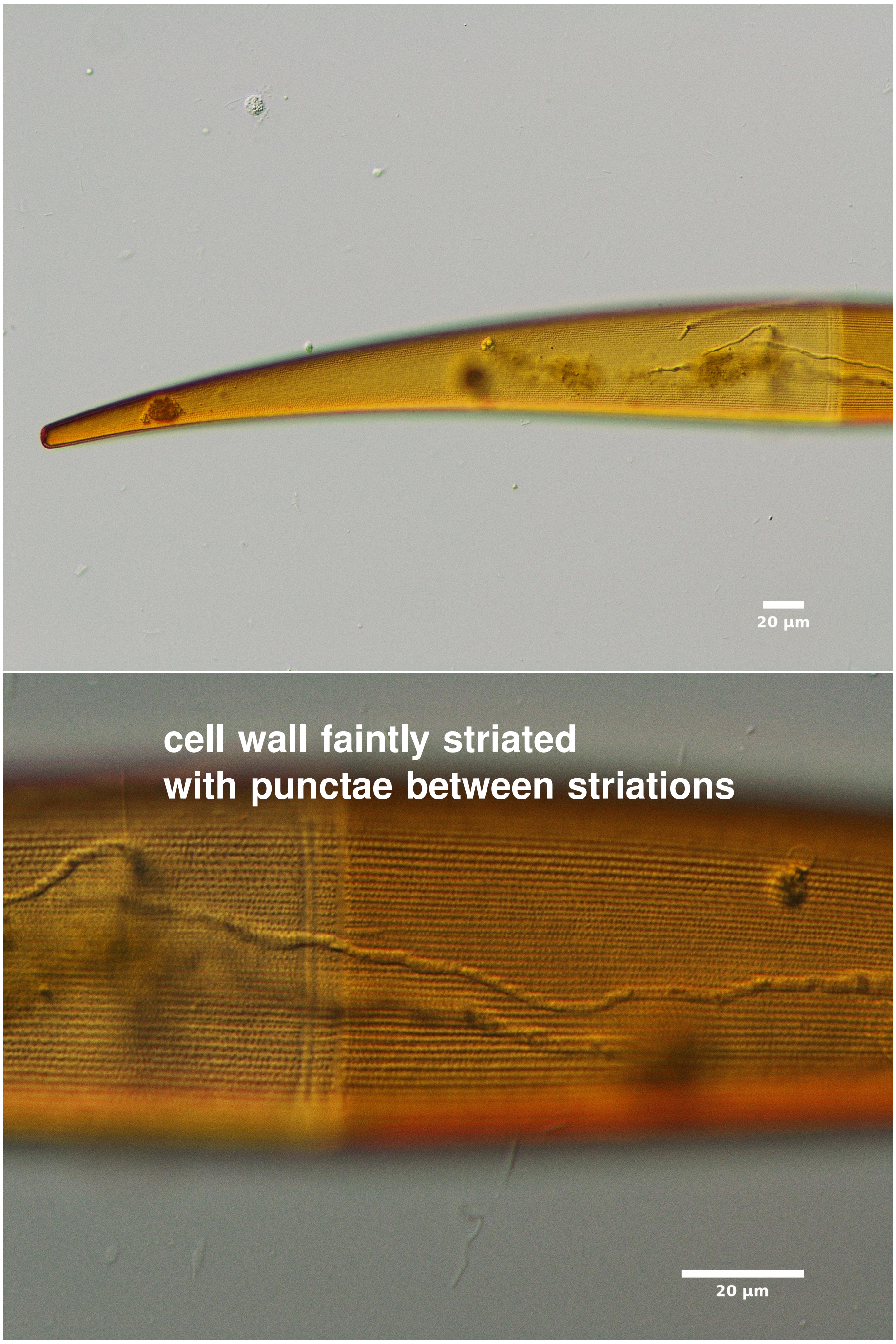


Figure 3.163: *Closterium ralfsii* var. *hybridum* (DIC/DIC), Summer Lake, Skagit County (upper/lower images).

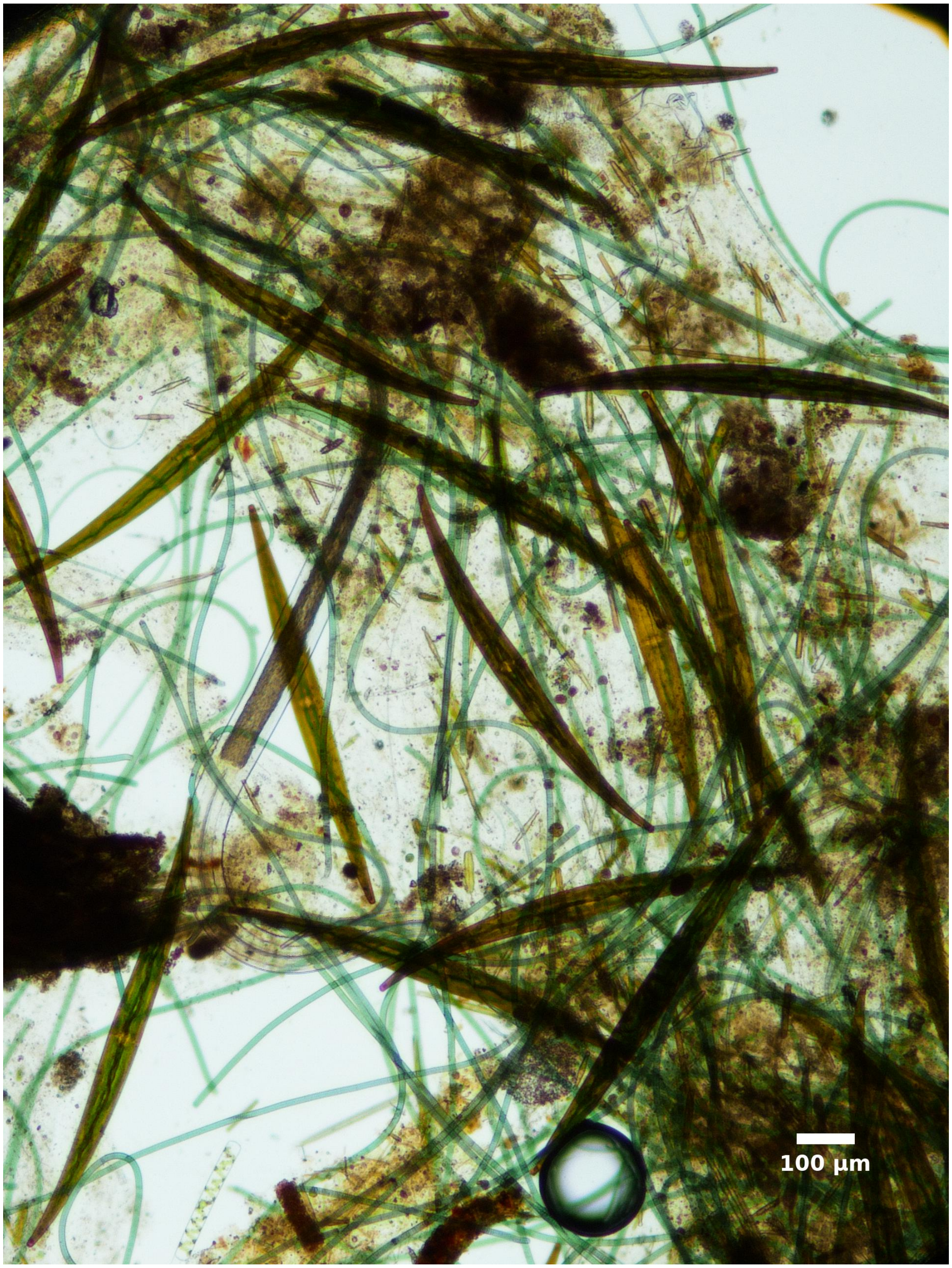


Figure 3.164: *Closterium ralfsii* var. *hybridum* bloom (bright field), Summer Lake, Skagit County.

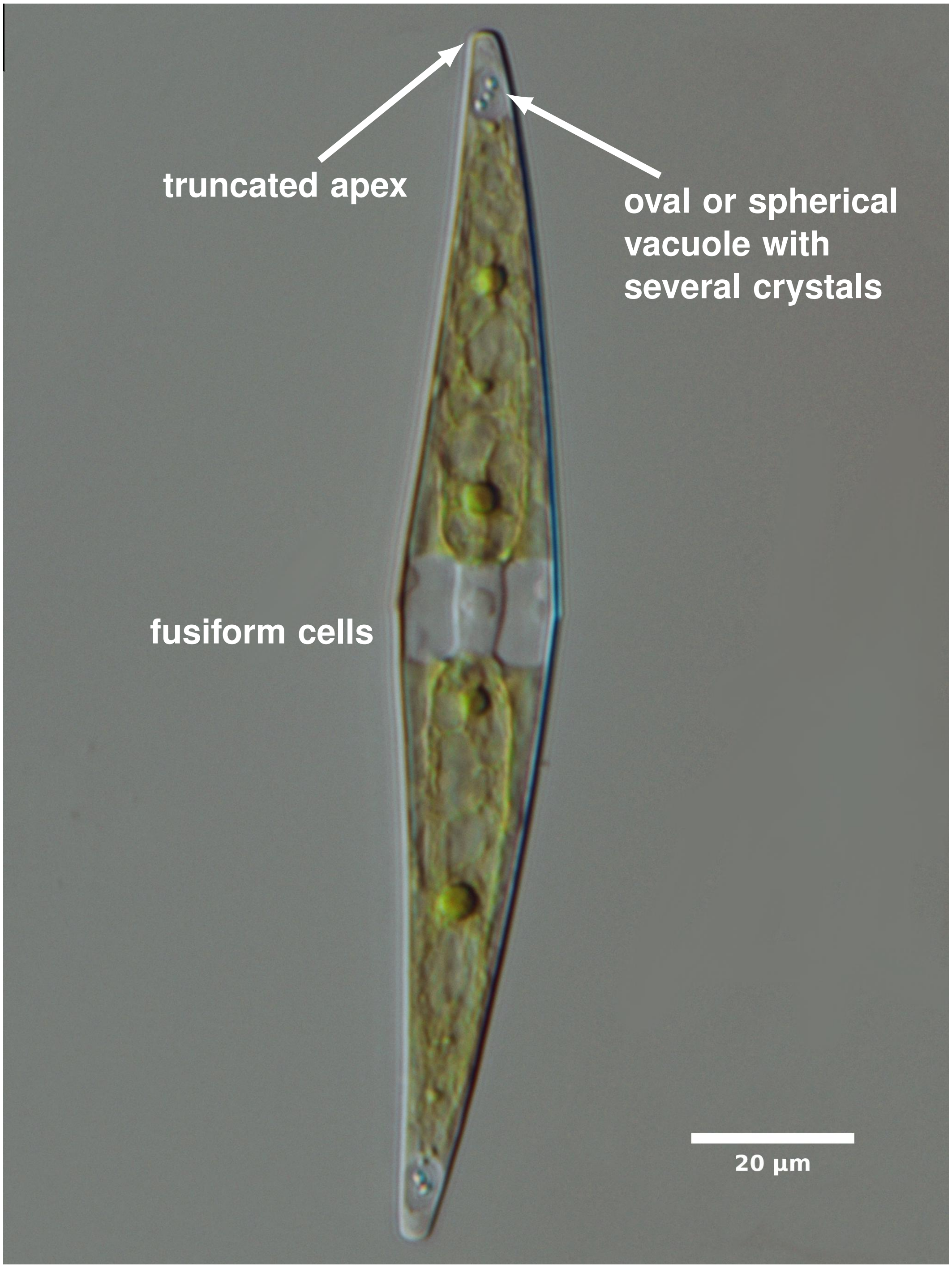


Figure 3.165: *Closterium* cf. *rectimarginatum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.166: *Closterium rectimarginatum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.167: *Closterium* cf. *rectimarginatum* (DIC), Lake Everett, Skagit County.

Figure 3.168: *Closterium* cf. *rectimarginatum* (bright field), Squalicum Lake, Whatcom County.

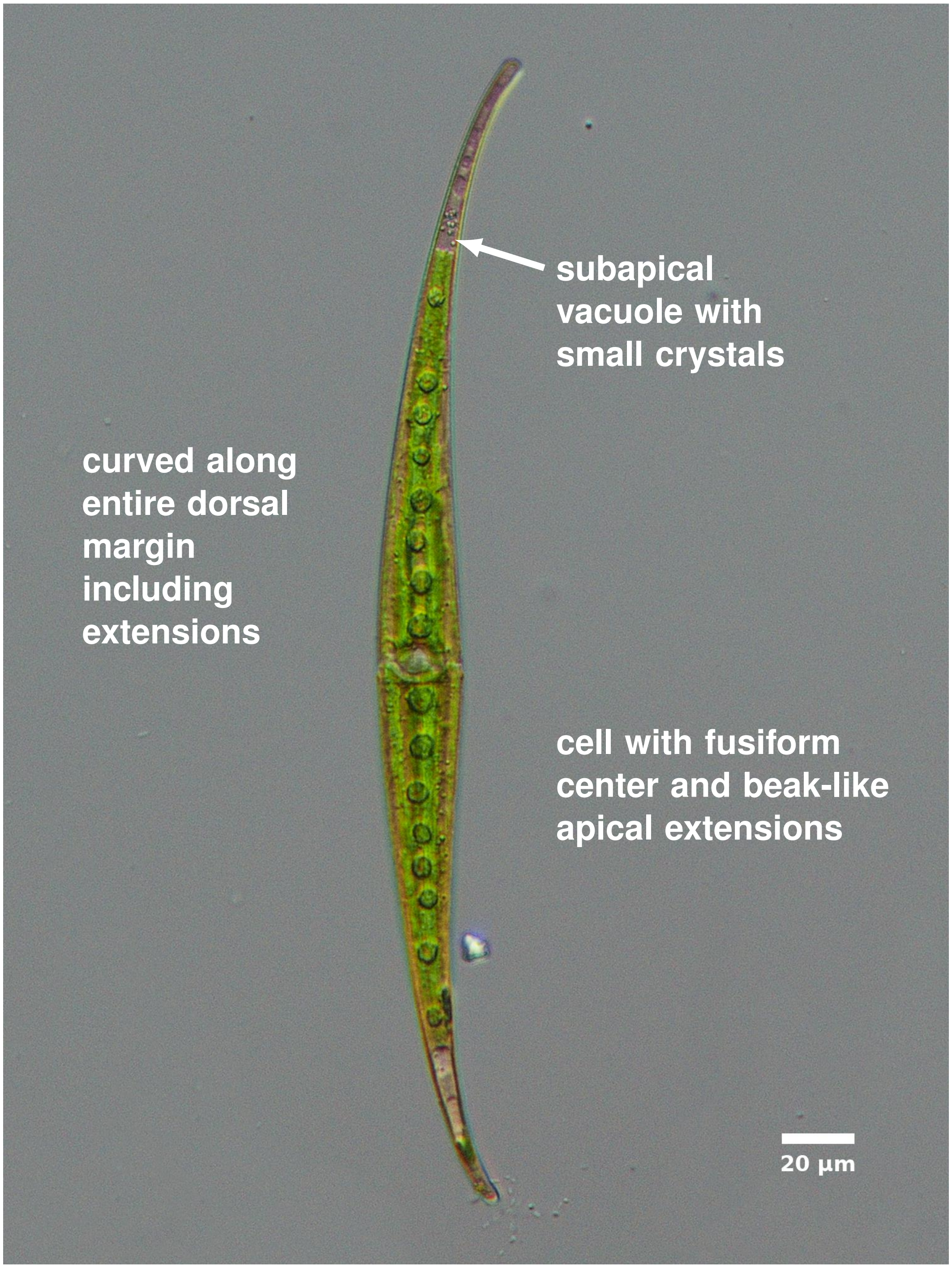


Figure 3.169: *Closterium rostratum* (DIC), Goat Lake, Mountain Loop Highway, Snohomish County.

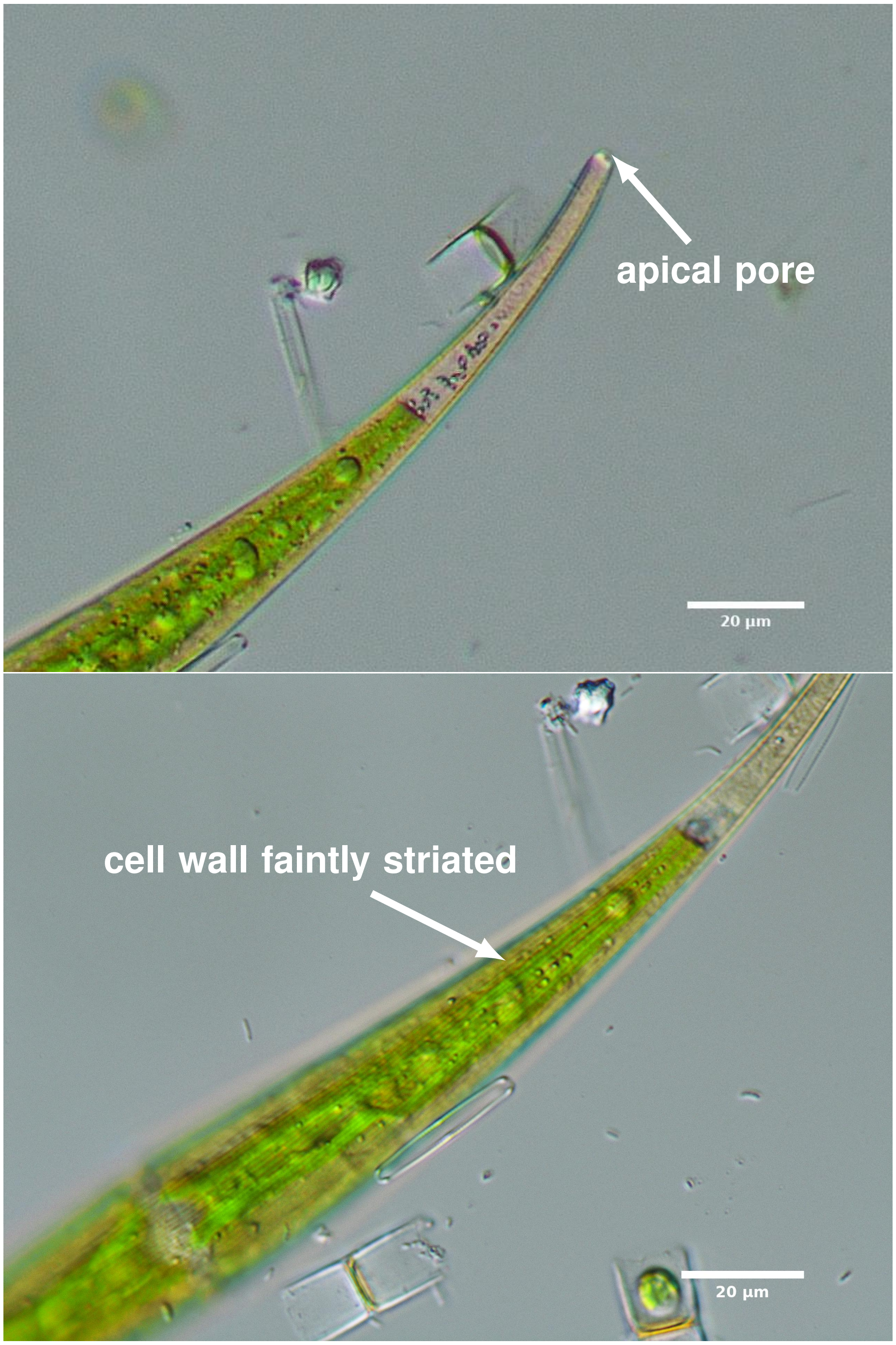


Figure 3.170: *Closterium rostratum* (DIC/DIC), side channel on Nooksack River, Whatcom County (upper/lower images).

Figure 3.171: *Closterium rostratum* (DIC), Beaver Lake, Skagit County.

Figure 3.172: *Closterium rostratum* (DIC), small residential pond, Whatcom County.

Figure 3.173: *Closterium rostratum* (DIC/DIC), cell variations in sample collected on same date, small pond along Military Road south of Tacoma, Pierce County (upper/lower images).

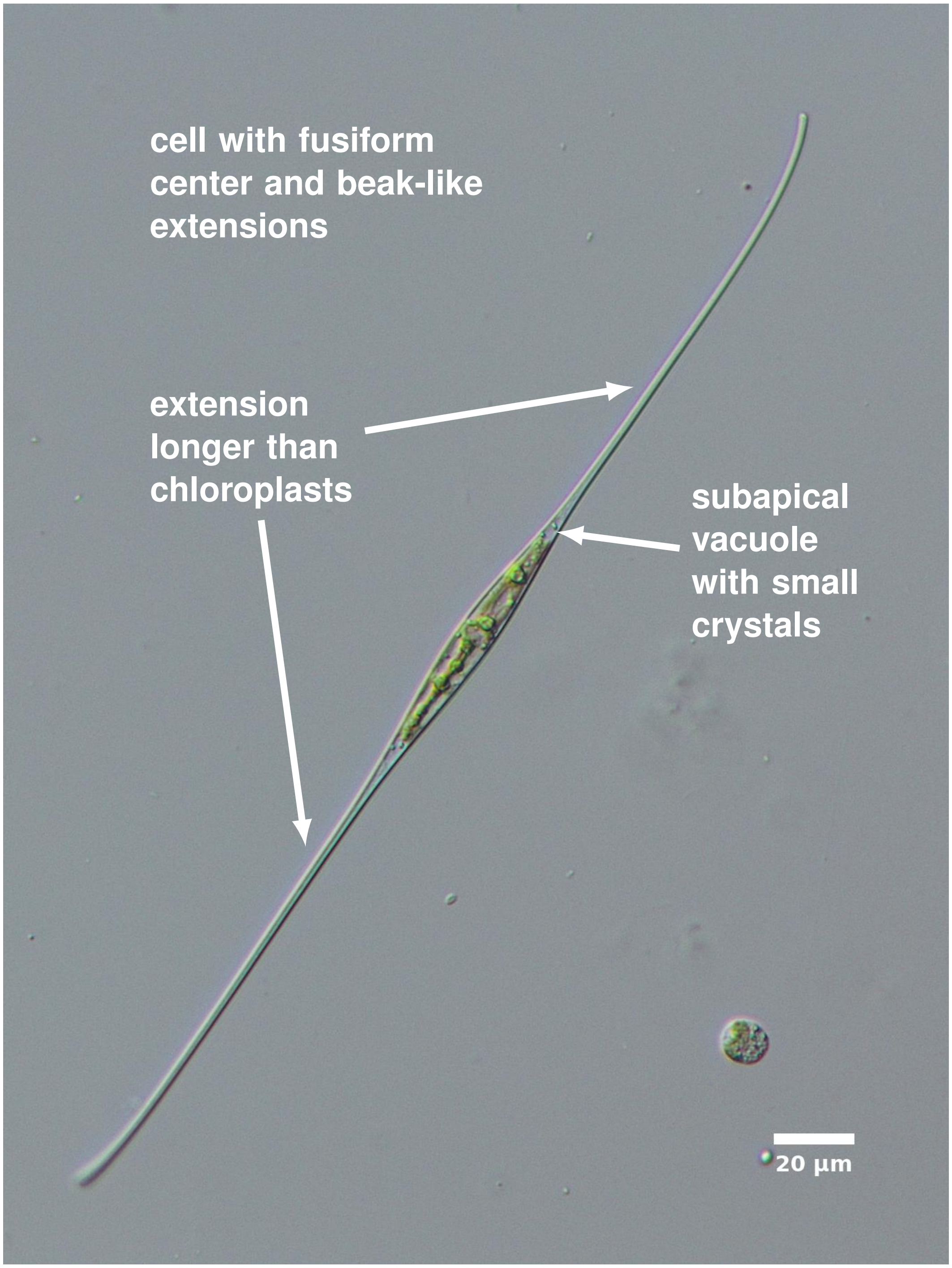


Figure 3.174: *Closterium setaceum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.175: *Closterium setaceum* (DIC/DIC), Summer Lake, Skagit County (upper/lower images).

Figure 3.176: *Closterium setaceum* (DIC), Myrtle Lake, Mountain Loop Highway, Snohomish County.

Figure 3.177: *Closterium setaceum* (DIC), Boardman Lake, Mountain Loop Highway, Snohomish County.

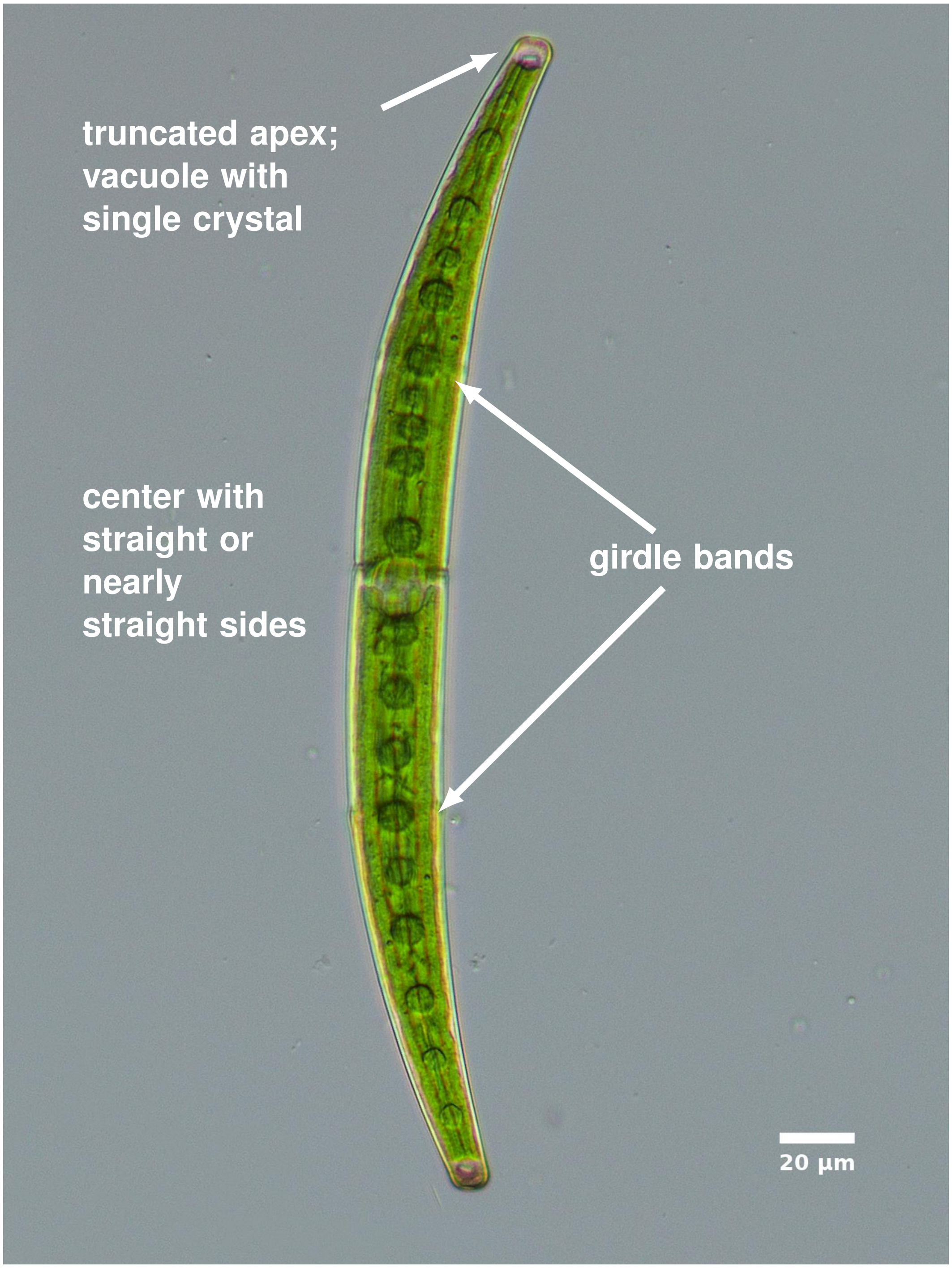


Figure 3.178: *Closterium striolatum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

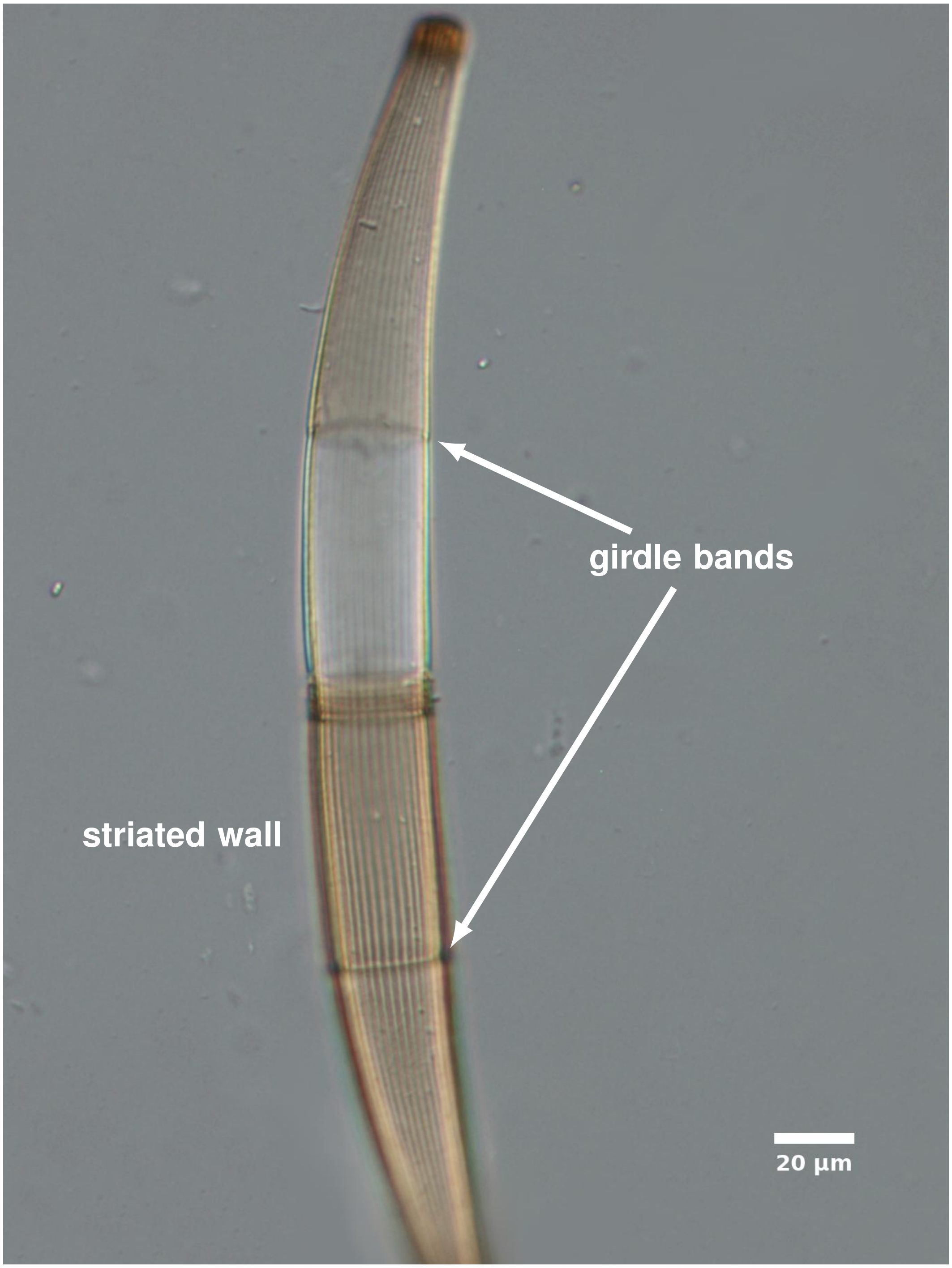


Figure 3.179: *Closterium striolatum* (DIC), Lake Evan, Mountain Loop Highway, Snohomish County.

Figure 3.180: *Closterium striolatum* (DIC/DIC), Mirror Lake, Whatcom County (upper/lower images).

Figure 3.181: *Closterium striolatum* bloom (DIC), Western Washington University storm water treatment pond, Whatcom County.

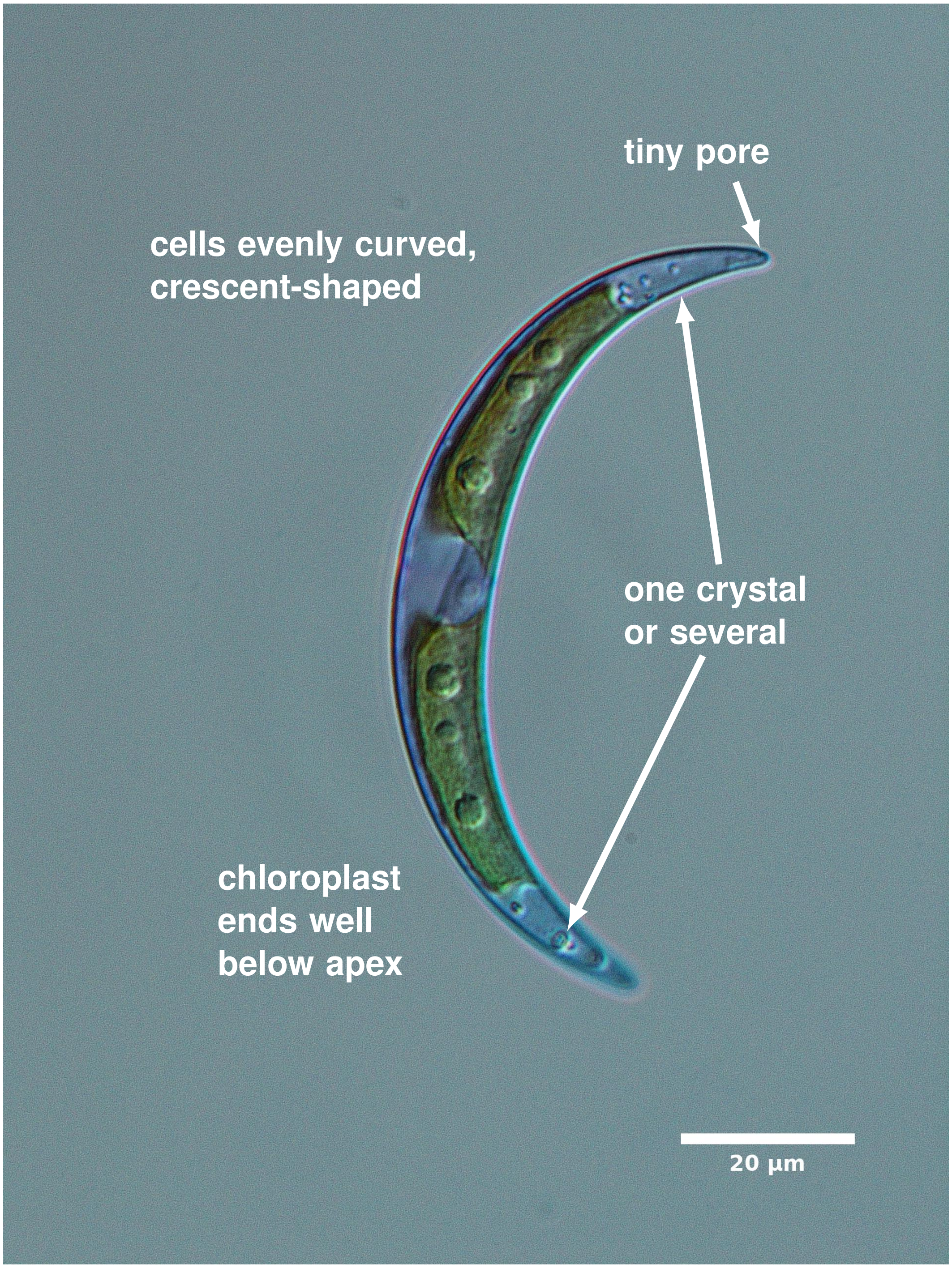


Figure 3.182: *Closterium venus* (DIC), stained with methylene blue, Hoag Pond, Whatcom County.

Figure 3.183: *Closterium venus* (DIC), Lake Everett, Skagit County.

Figure 3.184: *Closterium venus* (DIC), Beaver Lake, Skagit County.